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ABSTRACT

Laboratory and field measurements of photosynthesis, dark respiration and transpiration of *Gutierrezia sarothrae*, *Agropyron spicatum* and *Artemisia tridentata* were carried out in relation to plant water status and phenology, and microenvironmental parameters. Special emphasis was directed toward the elucidation of plant water stress effects on net photosynthesis. The relative gas exchanges of leaf versus stem material were also partitioned during these 1973 studies. Relative root growth rate studies were continued in the soil-root observation chambers installed in Curlew Valley, Utah, in 1972. There was an apparent shift of root growth activity from the upper to the lower soil horizons as the growing season progressed. The quantitative carbon balance of enclosed plant systems under laboratory conditions was carried out for *Atriplex confertifolia*, *Ceratoides lanata* and *Artemisia tridentata*. Approximately 85 to 90% of the carbon-14 used in these experiments could be accounted for in these balance trials. Substantial carbon-14 was expended in shoot and root system respiration.

In field studies in Curlew Valley, the translocation of carbon-14 to various plant parts for *Atriplex confertifolia* and *Ceratoides lanata* was carried out at three times during the growing season. To determine the allocation of carbon to above and below-ground plant parts on a community basis, similar carbon-14 plant tissue samples were analyzed and projected to a community basis using biomass samples for the *Atriplex*- and *Ceratoides*-dominated communities also taken in 1973. Carbon dioxide efflux of the soil surface in Curlew Valley during the growing season in communities dominated by *Atriplex confertifolia*, *Ceratoides lanata* and *Artemisia tridentata* was measured. Measurements were initiated in mid-April at which time there was a precipitous 10-fold decrease in efflux rates followed by low and consistent rates of CO_2 emission for the remainder of the growing season. To estimate underground productivity of these shrub species, the regrowth of roots into root-free soil cores originally excavated at the beginning of the growing season, 1972, was assayed. As another index of underground productivity, a new C^{14}/C^{12} dilution technique was employed in the *Atriplex*- and *Ceratoides*-dominated communities. This technique indicated substantial turnover of the underground system, particularly for *Atriplex confertifolia*. Preliminary estimates of foliage area index for the *Ceratoides lanata* and *Atriplex confertifolia* communities were also carried out. A preliminary synthesis of the carbon balance of the *Ceratoides lanata*- and *Atriplex confertifolia*-dominated communities is presented in this report along with an interpretative discussion.

INTRODUCTION

This process study of 1973 is comprised of several components. Gas exchange studies of Great Basin plants have been continued in 1973. This has included seasonal patterns of photosynthesis for *Gutierrezia sarothrae* and *Agropyron spicatum* based upon field measurements, and preliminary results of relationships between plant water potential, temperature, photosynthesis, and leaf resistances for *Gutierrezia sarothrae* and *Artemisia tridentata*. The relative gas exchanges of leaf versus stem material have also been partitioned in studies of these two species during 1973. These gas exchange studies have been designed to aid in refinement of aspects of the Desert Biome photosynthetic models now under construction.

This year a significant portion of our efforts has been directed toward elucidation of the relationship between shoot gas exchange and the growth and productivity of these plants, particularly on a community or land area basis. Translocation studies have been carried out both in the field and laboratory. Laboratory studies have been comprised of closed shoot-root systems where photosynthesis, translocation of photosynthates to various plant parts, and respiration of the above- and below-ground plant systems have been taken into account. This has been done for *Artemisia tridentata*, *Atriplex confertifolia* and *Ceratoides lanata*. In the field, extensive translocation studies of a similar nature have been carried out for the *Atriplex* and *Ceratoides* communities. On a community basis, allocation of fixed carbon to above- and below-ground plant parts has also been carried out for the *Ceratoides* and *Atriplex* communities. This has necessarily involved extensive biomass sampling of these two communities. To relate earlier field measurements of photosythesis of *Atriplex* and *Ceratoides* taken with gas exchange cuvettes to a community basis, preliminary estimates of foliage area indices of these two communities have been made during the growing season, 1973. Soil respiration studies of the *Atriplex*, *Ceratoides*, and *Artemisia* communities have also been undertaken during 1973 for the growing season. Estimates of shoot productivity during 1973 have been based upon new-growth/old-growth shoot ratios and litter production (field data collected by West (1972) and his associates). Below-ground productivity has been estimated by three different techniques: (1) regrowth of roots into soil cores previously excavated and replaced with root-free soil, (2) soil respiration studies, (3) a new radioactive carbon dilution technique.

The seasonal timing and the extent of root growth activity for *Artemisia*, *Atriplex* and *Ceratoides* as determined by soil observation chambers in the field have been continued on an extensive basis in 1973.

The first attempts to synthesize a carbon balance sheet for *Atriplex*- and *Ceratoides*-dominated communities are described herein, based on data of our group for the past few years and some data from N. E. West and colleagues.

Data and synthesis information contained in this report should contribute significantly to the photosynthesis and translocation submodels of the Desert Biome ecosystem-level modelling effort. In addition, the rudimentary carbon

balance sheets comprise a non-modelling synthesis which may help to elucidate carbon fixation and allocation patterns in two plant communities which grow in nearly identical abiotic environments.

OBJECTIVES

General goals of this project are: (1) to relate gas exchange rates of Great Basin plants to plant water status, plant phenology and to relevant environmental parameters in order to construct models of plant photosynthesis, dark respiration and water use, (2) to link plant gas exchange quantitatively with translocation, growth and productivity of higher plants on a community basis.

During 1973 our specific objectives were:

1. To gather additional information on the seasonal patterns of gas exchange of *Gutierrezia sarothrae* and *Agropyron spicatum*.
2. To carry out preliminary experiments on the effects of temperature and water stress on plant gas exchange and leaf resistances using *Gutierrezia sarothrae* and *Artemisia tridentata* as test species.
3. To analyze the contribution of leaf and stem components to plant gas exchange using *Gutierrezia sarothrae* and *Artemisia tridentata* as test species.
4. To analyze the extent and seasonal timing of root growth by field determinations for *Artemisia tridentata*, *Ceratoides lanata* and *Atriplex confertifolia*.
5. To determine a quantitative carbon balance of enclosed total plant systems under laboratory conditions for *Artemisia tridentata*, *Atriplex confertifolia* and *Ceratoides lanata*.
6. To determine translocation to various plant parts for *Atriplex confertifolia* and *Ceratoides lanata* in the field for three times during the growing season.
7. To determine CO_2 flux from the soil surface throughout the growing season in communities dominated by *Artemisia tridentata*, *Atriplex confertifolia* and *Ceratoides lanata*.
8. To determine the allocation of carbon to above- and below-ground plant parts on a community basis. This objective has included the need for biomass samples in the *Atriplex*- and *Ceratoides*-dominated communities.
9. To estimate underground productivity of all three prime species by regrowth of roots into root-free cores.
10. To estimate underground productivity of *Atriplex confertifolia* and *Ceratoides lanata* by a new C^{14}/C^{12} dilution technique.
11. To make preliminary estimates of foliage area index of *Ceratoides lanata* and *Atriplex confertifolia* communities.
12. To initiate a preliminary synthesis of the carbon balance of *Ceratoides lanata*- and *Atriplex confertifolia*-dominated communities.

METHODS

Field studies conducted during 1973 were carried out primarily in the Curlew Valley research area west of the Wildcat Hills where earlier studies of this project have taken place. In this area there exist communities dominated by *Artemisia tridentata*, *Atriplex confertifolia* and *Ceratoides lanata*. In terms of higher plant species these communites are nearly monospecific. Gas exchange studies for *Gutierrezia sarothrae*, *Artemisia tridentata* and *Agropyron spicatum* var. *inerme* were carried out at the mouth of Green Canyon approximately 6 km from the Utah State University campus. This site was also used in previous field studies reported in the 1972 progress report (Caldwell et al., 1973).

Gas Exchange

Gas exchange determinations for *Artemisia tridentata*, *Gutierrezia sarothrae* and *Agropyron spicatum* var. *inerme* were carried out in Cache Valley near Logan, Utah, during 1973. Instrumentation and methodology employed in these studies were described in detail in the 1970 progress report of the Desert Biome (Caldwell et al., 1971).

Photosynthesis, dark respiration and transpiration of *Artemisia tridentata*, *Gutierrezia sarothrae* and *Agropyron spicatum* were measured in the field in relation to pertinent micrometeorological parameters. The shoots of individual plants in the field were enclosed in Siemens gas exchange chambers for photosynthesis, respiration and transpiration measurements following monitored ambient conditions (DSCODES A3UCB43, CB44, CB97, and CB39), and also when the chambers were programmed for constant environmental conditions while varying one factor such as irradiation or temperature independently (A3UCB41, CB87, CB88, and CB39).

Pertinent microenvironmental parameters, plant water stress and phenology, and leaf area and weights are also logged under the above appropriate DSCODES. Air temperatures were measured by resistence thermometers, leaf temperatures with fine wire thermocouples, humidity by lithium chloride sensors calibrated against a Cambridge dewpoint hygrometer, and total short-wave irradiation with an Eppley pyranometer. In 1973 quantum sensors were used inside each chamber to determine total quantum flux between 400 and 700 nm (Biggs et al., 1971). Plant water stress was measured with a Scholander pressure bomb, and leaf area with a photoelectric planimeter (Caldwell and Moore, 1971).

In 1973, detailed laboratory and field studies were carried out to determine the exact nature of the effects of plant water stress on gas exchange of *Artemisia tridentata* and *Gutierrezia sarothrae*. Field studies on irrigated versus non-irrigated plants of each species in the same phenological stage were carried out in August, 1973. Additional studies on potted plants of each species over a wide range of plant water potentials were made to corroborate the field experiments. Relationships have thus been defined between plant water potential and such things as dark respiration rates, net photosynthetic rates and leaf resistances to gaseous flux.

An attempt was also made in 1973 to determine magnitudes of gas exchange of different above-ground plant organs (stems vs. leaves) of *Artemisia tridentata* and *Gutierrezia sarothrae*. These studies were carried out mainly on potted plants in the laboratory, and involved taking gas exchange measurements of intact and defoliated stems. Results of this experimentation should elucidate the relative contributions of stems and leaves to total above-ground plant gas exchange. These results may also provide a possible basis for correction of gas exchange rates of previous years' research which have been based solely on leaf biomass while ignoring stem material present in the plant sample. This, however, only turns out to be significant for *Gutierrezia*.

Root Growth Studies

To determine the timing of root growth in the field, the six soil root observation chambers which were installed in the *Atriplex*-, *Ceratoides* - and *Artemisia*-dominated communities in 1972 were used again in 1973. Soil thermocouple psychrometers for soil water potential determinations and soil thermocouples for soil temperature measurement were again installed adjacent to the inclined plexiglass observation panes in the immediate vicinity of the observed root zone and in the undisturbed community approximately 1 m away. Details of the root observation chambers are in the 1972 progress report (Caldwell et al., 1973). In addition to observing the seasonal timing of root growth in these three species, relative root elongation at various depths in the soil profile was also determined by measurement. This was then calculated on a relative growth rate basis. Although these growth rate determinations cannot be equated with root productivity or growth rates in the undisturbed soil, on a relative basis they do indicate the extent of activity at various times of the year at different depths.

Soil Respiration

Field measurements of carbon dioxide efflux from the soil surface (A3UCB25) were also carried out between April and December, 1973, in the *Ceratoides*, *Artemisia* and *Atriplex* communities. Inverted No. 10 size cans (covering 0.02 m^2 of surface area) were placed on the soil surface with the walls of the can penetrating the soil to a depth of approximately 5 cm. These were insulated and covered by a waxed cardboard cover painted a light color. Sixteen of the CO_2-collection units were located in each community. In each case, half were placed between individual plant canopies and half directly under the canopies. For absorption of CO_2 from the soil, 50 ml of 0.3 N NaOH was placed into an open jar inside each collection vessel. The NaOH was titrated before and after each collection period to calculate the amount of CO_2 absorbed. There were 12 collection periods between April and December of 1973. During each collection period CO_2 efflux from layers of sterilized soil was also determined in the field. This served as a control to determine the approximate amount of CO_2 diffusion that might take place laterally within the soil profile, and also any abiotic release of CO_2 in these soils which are very high in carbonates. Soil and air temperatures were also recorded within the collection vessel at the beginning and end of each period to compare with conditions outside the vessel. Heating of the soil surface underneath the collection vessel relative to adjacent soil areas was only noticeable during the warmest part of the summer, in July and August. At this time, soil surface temperatures were only 1 to 2 C above those outside the vessel. At depths of 1 cm, temperatures were the same. The location of the collection vessels was changed each collection period.

Translocation and Carbon Allocation Studies in the Field

The partitioning of fixed carbon to various plant parts and allocation of this carbon to above- and below-ground productivity on a community basis (A3UCB20) were studied for *Ceratoides lanata*- and *Atriplex confertifolia*-dominated communities. In order to carry out such studies on a community level, it was necessary to treat a unit ground-area of the community rather than to work on an individual plant basis. Working on an individual plant basis is impossible because it is not feasible to extract all of the root material of any single individual plant since these overlap significantly with neighboring plant roots. Furthermore, to treat isolated plants growing apart from the community is unrealistic since there is a minimal amount of root interaction with other plants. At three times during the growing season, air-tight plastic film tents were erected over 2.2 x 2.2 m plots in the *Atriplex* and *Ceratoides* communities. This was done in April, July and September of 1973. These experiments were started at dawn with $C^{14}O_2$ liberated inside the tent by reacting labeled barium bicarbonate with lactic acid. During the course of the experiment the air inside the tent was mixed with a small fan. Plants inside the tent were allowed to assimilate the radioactive CO_2 for 4-5 hr. Leaf, soil and air temperatures were recorded. When leaf temperatures reached 45 C the labeling was terminated and the tent was removed to prevent any heat damage to the plants. In July it was necessary to use one to two layers of cheesecloth screening to delay the temperature increase. This technique permitted labeling of the rather large experimental plot without expensive temperature control and without undue damage to the plants. Plant samples were taken 72 hr after the application of $C^{14}O_2$ and again at the end of the season in September. To determine concentrations of C^{14} in various organs of the plant shoot, several above-ground plant portions were harvested from the plots and separated for further processing and counting. Root material was harvested within the labeled plot by soil coring using an 8-cm diameter orchard auger within the central 1.1. m x 1.1. m area of the labeled plot where all roots were presumed to originate from plants within the 4.8 m^2 labeled plot.

To determine the allocation of fixed carbon on a community basis to above- and below-ground plant parts, the same samples and test plots were employed. However, it was necessary also to determine community biomass in each

case in order to extrapolate concentrations of C^{14} to quantities of carbon per unit ground area. Biomass sampling was carried out by selecting a series of random plots, 4.8 m^2 in the *Atriplex* community and 1.2 m^2 in the *Ceratoides lanata* community. All above-ground biomass was collected, separated into current year's and previous year's growth fractions, dried and weighed. Underground biomass was determined by a series of soil cores using an 8-cm diameter orchard auger. Twelve to 16 plots were used in a community with 3 to 8 soil cores in each plot. Plot and core numbers were increased until the mean could be estimated with a coefficient of variation of $\pm 15\%$. The techniques follow very closely those of Bjerregaard (1971).

General Combustion and Counting

In all work with carbon-14, recommended health and safety precautions were followed. Disposal of residual $C^{14}O_2$ in the field was carried out at AEC-specified concentrations. The grinding and other processing of radioactive plant samples in the laboratory was carried out in closed hoods under negative pressure. All plant samples were dried and ground in a modified coffee mill and stored for subsequent combustion and counting. Samples of 150 mg were normally combusted. Combustion of plant parts was carried out inside a 500 ml suction flask with a side arm. For reasons of safety (due to expansion during combustion) a balloon was fixed to the side arm. Vegetative samples of 50-250 mg each were weighed and wrapped in black lens tissue. They were then suspended inside the flask on a piece of wire attached to the flask stopper. Also, the stopper had a piece of glass tubing inserted through it over which a syringe cap could be sealed. Before combustion the flask was thoroughly flushed with pure oxygen. Next, a strong beam of a focused slide projector lamp was directed onto the sample, resulting in combustion. After allowing the gas to mix well, a 20 ml aliquot of gas was removed with a syringe and injected into a syringe-capped scintillation vial containing 2 ml of ethanolamine (CO_2 absorber). After 24 hr the syringe cap was removed from the vial and 20 ml of scintillation fluid was added. This scintillation "cocktail" contained 460 ml of Toluene, 270 ml Methanol, 5 g PPO, and 100 mg POPOP. The vial was allowed to sit for 5 hr to eliminate any chemiluminescence and then analyzed in a liquid scintillation counter (Nuclear-Chicago) for carbon-14 content.

A large high-temperature furnace was employed to combust soil samples. A soil sample of from 1 to 10 g was placed inside a porcelain "boat" and slipped inside a quartz (Vycor) tube. The tube was heated to 900 C in an atmosphere of O_2 for combustion. In this "open" system the CO_2 was flushed out at a flow rate of 0.015 l min^{-1} through a series of 3 scintillation vials each containing 2 ml of ethanolamine. After an hour, the vials were removed and to each was added 20 ml of the "cocktail".

Some of the experiments in this report involved absorbing the $C^{14}O_2$ in 0.3 N NaOH. When this was the case, a 0.5 ml aliquot was removed and mixed with 20 ml of "cocktail" for counting.

Laboratory Carbon-14 Balance Experiments

Plants of all three species, *Atriplex confertifolia*, *Artemisia tridentata* and *Ceratoides lanata*, were collected from Curlew Valley and potted. They were placed in the greenhouse and watered until the soil was completely saturated. Thereafter they were watered every 3 to 4 days. Daytime temperature was 24 C and nighttime temperature 16 C. Plants used in experiments were generally in a late spring condition with photosynthetically active leaves (A3UCB23).

Each pot was encased in a 19-liter plastic film bag and sealed around the stem base with string. Using tygon tubing, an entrance and exit port were installed in the bag. A manometer was used to test the bag system for air tightness.

The aerial portion of the plant was sealed in a Seimens gas exchange chamber (see Caldwell et al., 1971) and the chamber temperature adjusted to 25 C during the day and 15 C at night. The light source was four Sylvania, cool-lux lamps with total intensity generally around 700 μeinsteins m^{-2} sec^{-1}. The flow system was "open" with an infra-red gas analyzer in the circuit to measure CO_2 uptake or release and thus photosynthesis or respiration.

In order to label the plant, the "open" system was changed to a "closed" one and a measured amount of $C^{14}O_2$ was introduced into the chamber using a syringe. The plant was allowed to fix the $C^{14}O_2$ for 3 hr and then all air was flushed from the chamber at 3.0 l min^{-1} for 15 min. By trapping the flushed $C^{14}O_2$ in ethanolamine and counting it we determined approximately the amount fixed by the plant. Immediately following the flush, collection of respired $C^{14}O_2$ was begun, using ethanolamine as a CO_2 absorber.

Respired $C^{14}O_2$ coming off the soil was collected by using a pump and a gas washing bottle filled with 50 ml of 0.3 N NaOH, all in a "closed" system.

Experiments were set up using a 12-hr photoperiod. At the beginning of each new period, $C^{14}O_2$-collection vessels were changed.

At the end of each experiment the plant was harvested. Above- and below-ground portions were separated and frozen. After 1-2 weeks, separation of plant parts into leaves, buds, roots, etc., was carried out. All parts were then dried, weighed, combusted, and counted. Combustion and counting were carried out as outlined in the preceding section of the Methods.

Root Reinvasion into Soil Cores

One technique for estimating root productivity (A3UCB26) involved a measure of roots reinvading soil cores (Milner and Hughes, 1968).

The study began on April 1, 1972. Using an 8-cm soil auger, 18 holes, 50 cm deep, were bored in each of the three communities (*Atriplex*, *Artemisia* and *Ceratoides*). Care was

taken to remove the soil from each hole in increments of 10 cm each. Thus, mixing of soil from different depths was minimized. Each of these increments was then individually sieved free of most roots using a sieve of 1 mm pore size. To determine the average amount of root material left in the soil after this treatment, a separate experiment was conducted. Nine holes were drilled outside our experimental area (20 m away) and the soil taken to the laboratory. The soil was subjected to the same treatment as above except that a second wet sieving technique was used to determine the amount of root which passed through the first sieve. The soil was mixed with an excess of water. Roots either floated or were held momentarily in suspension while the water was poured through a sieve with a pore size of 0.5 mm. Roots from both sievings were washed well, dried and weighed.

After sieving the experimental soil with the 1 mm sieve in the field, it was treated in two fashions. Soil from 9 of the 18 holes was replaced in the hole in the same depth sequence as it had been removed. The remaining 9 samples were placed inside nylon socks (60 cm x 8 cm with 0.5 mm pore size) in the same depth sequence and the socks were lowered back into their respective holes. Locations of holes with or without socks were recorded and marked.

On September 17, 1973, harvesting was carried out. The socks were excavated and the holes without socks were re-bored. The soil from these treatments was taken to the laboratory for sieving. The soil was sieved dry with the 1 mm sieve and wet with the 0.5 mm sieve. Roots trapped by either method were washed well with water, dried and weighed.

$^{14}C/^{12}C$ Dilution Experiments

As another index of underground productivity for what might be termed root-turnover (A3UCB27), a new technique utilizing dilution of carbon-14/carbon-12 in cell-wall tissues of roots was employed for the first time this year. Theoretically, if the underground root mass is sufficiently well sampled, ratios of C^{14}/C^{12} in cell-wall tissues can be determined early in the season after the first labeling and again at a later point in time from the same plot. The dilution or decrease in this ratio reflects input of new cell-wall carbon into this root mass. This new carbon in turn reflects root productivity or turnover. There are, of course, many assumptions and potential sources of error involved with this C^{14}/C^{12} dilution technique which will be covered more fully in the Discussion section.

Eight days after the April labeling of the *Atriplex* and *Ceratoides* community plots used in the translocation experiments, 7 additional soil cores were removed from both plots and separated into 3 depth fractions. An equal number of cores were removed from the same plots on September 18, 1973.

Using a 0.5 mm pore size sieve and a stream of cold water, roots were removed from the soil and washed three times with water. Two categories of roots were used in the analysis, live and live + dead. In order to obtain live roots, we employed visual inspection and a geiger counter. This technique worked well with the larger roots but was clearly not satisfactory for smaller ones.

After separation of the roots, cell wall matter was extracted (Van Soest and Wine, 1967) and dried. This was then combusted and counted using the same methods described earlier.

Foliage Area Index

Although not originally a goal of this project, it is evident that in order to extrapolate earlier gas-exchange measurements of these shrub species (taken with cuvettes on branches of the plants) to a community basis, information concerning foliage-area indices of these communities is necessary. Therefore, preliminary attempts were carried out in 1973 to determine the foliage area index of the *Ceratoides* and *Atriplex* communities. For *Ceratoides*, foliage-area index was determined by the inclined point quadrat technique (Warren-Wilson, 1960) with a pin-angle of 32.5°.This was carried out for a series of 17 plots in the *Ceratoides* community. *Atriplex confertifolia* is a much larger shrub and much more unevenly spaced in the community. In this situation, inclined point frames were again used, however, for individual plants (Warren-Wilson, 1965). This turned out to be extremely time-consuming and therefore only four shrubs could be analyzed in detail. By this technique, foliage-area index for the crown projection of these shrubs was determined. In order to estimate the area of crown projection in the *Atriplex* community, photographs were taken of 20 plots from approximately 4 m height. The crown projection area was then later determined from the photographic prints.

RESULTS

Gas Exchange Studies

Seasonal measurements of plant gas exchange have been most successfully represented as rates for each phenological stage of the plant. Accordingly, phenological codes were developed for cold desert species studied in previous years (*Artemisia tridentata*, *Atriplex confertifolia* and *Ceratoides lanata*). The following numerical indices were established for the species *Gutierrezia sarothrae* and *Agropyron spicatum* var. *inerme*:

Gutierrezia sarothrae

1. Winter dormancy.
2. Regreening of short shoots formed previous autumn (late April-early May).
3. Elongation of short shoots; leaf enlargement (mid-late May).
4. Maximum leaf development; floral buds emerge (early-mid June).
5. Leaf dieback begins; floral buds developing (late June, July).
6. Maximum dieback of large leaves along long shoots; flowers developing (August).
7. Flowering; short-shoot initiation at base of plant (September).

8. Fruit developing (early-mid October).
9. Fruit dissemination; dieback of long shoots (late October-November).

Agropyron spicatum var. *inerme*
1. Winter dormancy.
2. Growth initiation (late April-early May).
3. 2-3 leaf stage; spikelet initiated (mid-late May).
4. 4-5 leaf stage; spikelet fully formed (June).
5. Leaf dieback; summer dormancy initiated (July).
6. Hard seed (August).
7. Seed scatter (September-early October).

Seasonal pattern of gas exchange of *Gutierrezia sarathrae* and *Agropyron spicatum* var. *inerme* in the field are reported in Figures 1-4 (A3UCB87, CB88 and CB39). Figures 1 and 2 give responses of net photosynthesis under conditions of constant irradiation and variable temperature for the two species in various phenological stages. Figures 3 and 4 show variations in rates of dark respiration with temperature changes.

Responses of net photosynthesis to differences in plant water potential under conditions of constant irradiation and variable temperature for *Gutierrezia sarothrae* and *Artemisia tridentata* are shown in Figures 5 and 6. Similarly, responses of dark respiration to the same variables for these two species are given in Figures 7 and 8. These experiments were carried out on irrigated and non-irrigated plants in the same phenological stage in the field (A3UCB39). Figure 9 gives a "typical" two-day curve of plant water potential, measured by pressure bomb, for *Artemisia tridentata* and *Gutierrezia sarothrae* in the field.

Figures 10 and 11 show responses of net photosynthesis, stomatal diffusion resistance (r'_a and r'_s), and mesophyll resistance (r'_m) to variations in temperature under constant irradiation for *Gutierrezia sarothrae* and *Artemisia tridentata*. Both species were at approximately the same plant water potential. This experimentation was carried out on potted plants in the laboratory (A3UCB39).

Results of laboratory defoliation experiments are shown in Figures 12 and 13 for *Artemisia tridentata* and *Gutierrezia sarothrae*. Net gas exchange rates for stems, leaves and entire samples are given under conditions of constant irradiation and variable temperature (A3UCB39). Figures 14 to 16 show differences in apparent rates of leaf net gas exchange (net photosynthesis and dark respiration) encountered when adjustments are and are not made accounting for stem gas exchange activity of the plant sample. These three figures were derived from the laboratory defoliation experiments, and will be explained in the Discussion.

Most of the gas exchange study results reported in this 1973 report are from measurements taken during the past year. However, in Figures 17 to 22, previously unreported relationships between soil moisture potential and photosynthesis of *Atriplex confertifolia* and *Ceratoides lanata* are depicted. These are from measurements taken with potted plants in late summer condition in the laboratory. Regression lines determined by least squares analysis are shown for each set of data points. Soil moisture potentials were measured by four to five thermocouple psychrometers located in each pot. These data were taken in the early fall of 1970.

Laboratory Carbon-14 Balance Studies

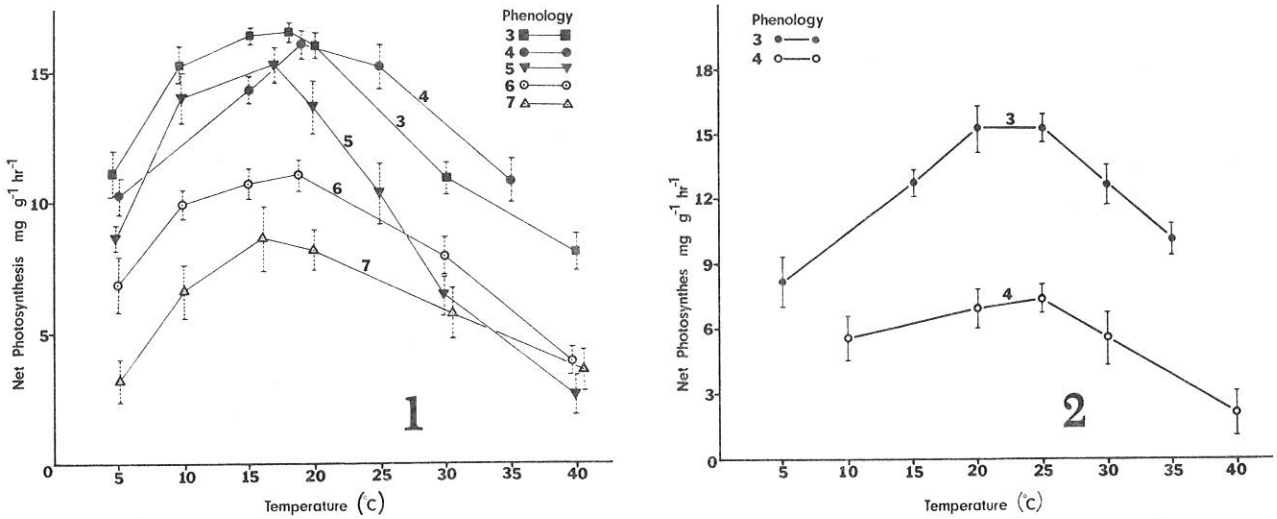
The laboratory carbon-14 balance studies are summarized in Figures 23 through 27 (A3UCB23). Each figure represents the result of an individual plant study. There was often substantial variability between plants owing largely to the exact growth stage of the plant. Although all plants were taken in an early spring condition when leaves were photosynthetically active, they varied as to whether or not actual shoot elongation and bud swelling was taking place. Similar experiments were carried out on other plants; however, only these were sufficiently controlled for reporting. By accounting for all gaseous carbon fluxes and carbon-14 in various plant parts as well as residual carbon in the soil remaining after root extraction, 84 to 91% of the calculated fixed carbon could be accounted for in these closed system studies.

That unaccounted carbon-14 undoubtedly is the result of some measurement errors, small gaseous leaks, particularly from the below-ground system, and inability to harvest all carbon from the soil-root system. The patterns and absolute magnitude of carbon-14 efflux from the root/shoot systems of these plants are represented in Figures 28 through 32. Considerable diurnal variation is apparent. Refixation of $C^{14}O_2$ respired by the shoot system is considered to be minimal since a high flow rate (3 liters min^{-1}) was always employed. Carbon dioxide efflux from the root systems was never allowed to enter the shoot chamber.

Field Translocation Studies

Tables 1 through 4 contain summarized results of the field carbon-14 translocation studies (A3UCB20). This is represented in Tables 1 and 2 in terms of actual disintegrations min^{-1} of carbon-14 per mg dry weight of plant samples. The variability between the three plants used in each case can also be noted in these tables. The results were surprisingly consistent for any particular time period. The columns labeled April, July and September represent the results of carbon-14 partitioning 72 hr after the photosynthetic incorporation of $C^{14}O_2$. The columns labeled September-April treatment and September-July treatment represent the results of carbon-14 partitioning taken in September from plots originally labeled in April and July, respectively.

Tables 3 and 4 depict the average percentage of partitioned radioactive carbon to various plant parts. These are derived from Tables 1 and 2. As much as was possible, the dry weight of the shoot and root systems refers to living biomass as obviously dead and decomposing roots were omitted from the samples. However, at the time these data were collected there was no definitive method for determining live from dead root material, particularly for the small root fractions. Therefore, root dry weight material



Figures 1-2. Net photosynthesis of *Gutierrezia sarothrae* at five phenological stages (1) and *Agropyron spicatum* var. *inerme* at two phenological stages (2) through a growing season. Experiments were carried out on field plants *in situ* under conditions of constant irradiation (1100 microeinsteins/m^2/sec) and varying leaf temperatures. Values are means of 3-6 plants measured, shown ± one standard deviation (DSCODES A3UCB87, 88 and 39).

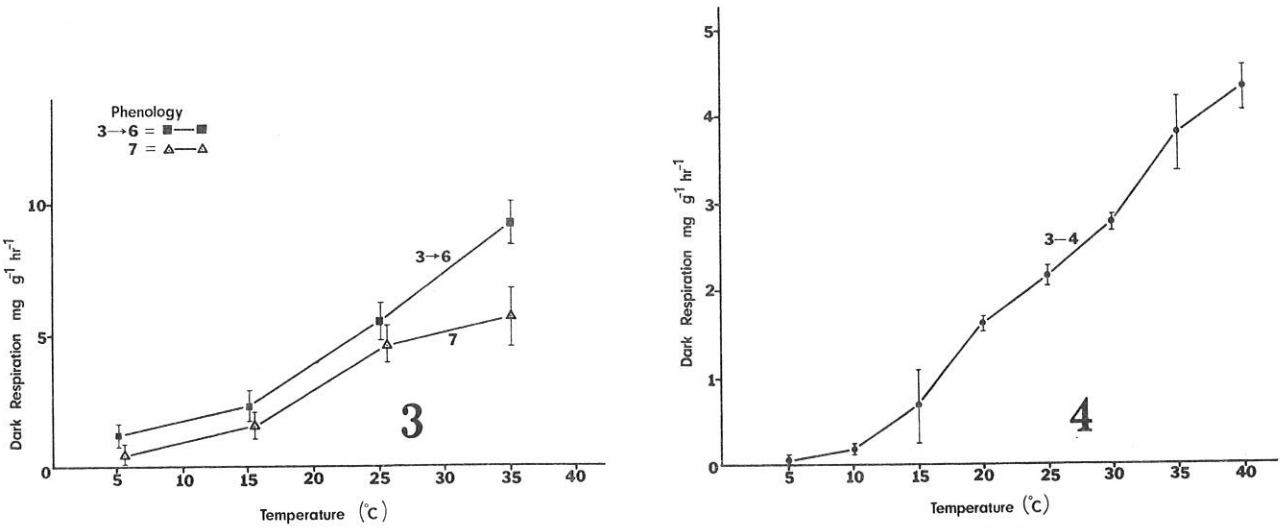
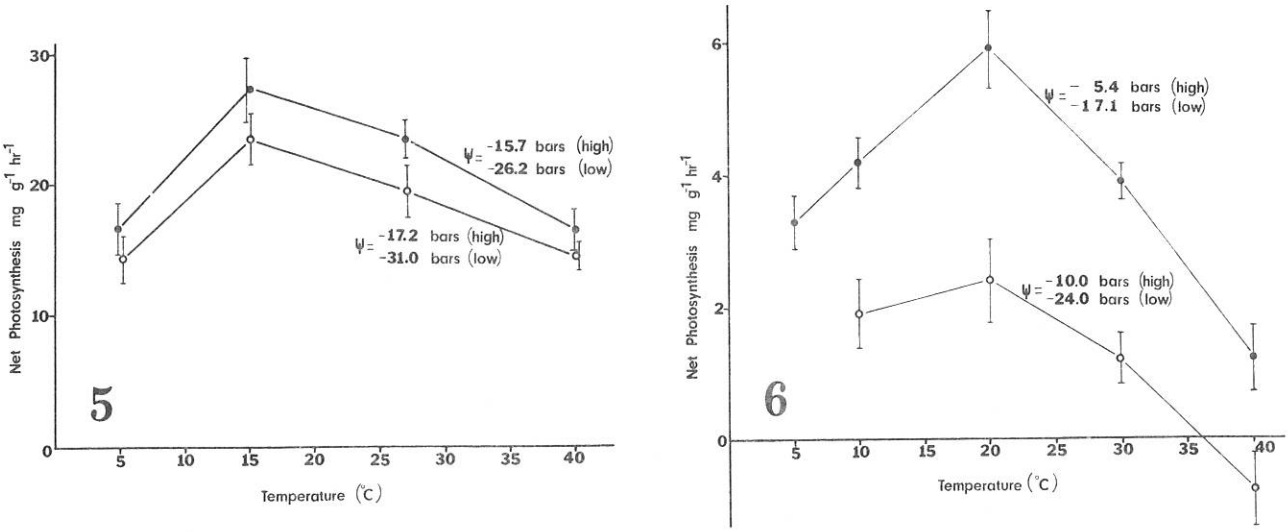
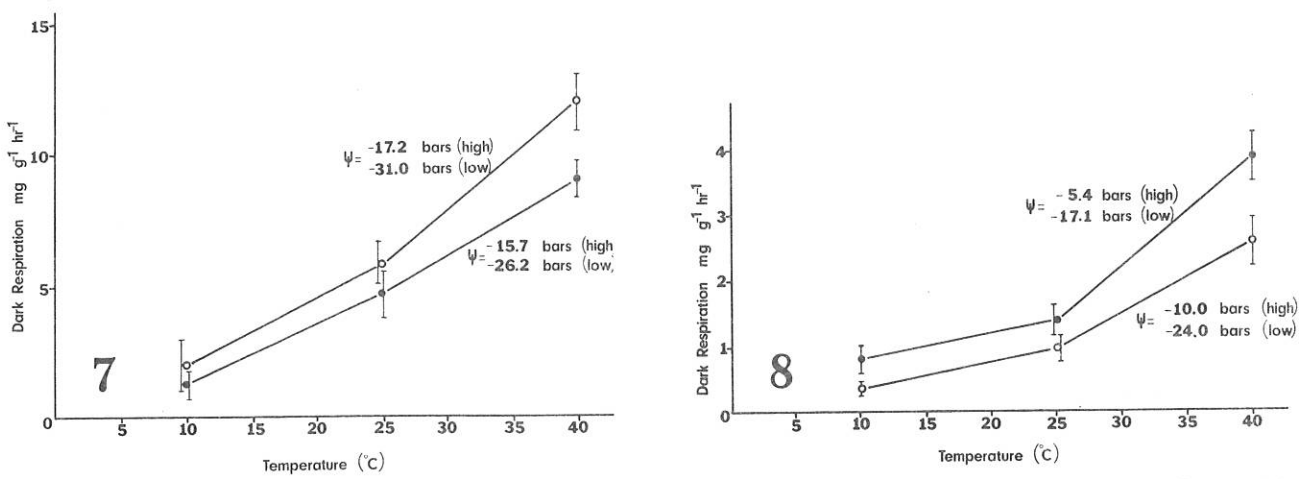


Figure 3-4. Dark respiration of *Gutierrezia sarothrae* at five phenological stages (3) and *Agropyron spicatum* var. *inerme* at two phenological stages (4) through a growing season. Experiments were carried out on field plants *in situ* at night under conditions of varying leaf temperature. Values are means of 3-6 plants measured, shown ± one standard deviation (A3UCB87, 88 and 39).



Figures 5-6. Effects of plant water potential on net photosynthesis of *Gutierrezia sarothrae* (5) and *Artemisia tridentata* (6). Experiments were carried out on irrigated (•—•) and non-irrigated (∘—∘) field plants *in situ* at the same phenological stage (6-August; see RM 73-13 for *Artemisia* phenophase) under conditions of constant irradiation (1100 microeinsteins/m^2/sec) and varying leaf temperatures. Water potentials (ψ) for each treatment are given adjacent to the appropriate lines. Values are means of 3-4 plants measured, shown ± one standard deviation (A3UCB39).



Figures 7-8. Effects of plant water potential on dark respiration of *Gutierrezia sarothrae* (7) and *Artemisia tridentata* (8). Experiments were carried out on irrigated (•—•) and non-irrigated (∘—∘) field plants *in situ* at the same phenological stage (6-August: see RM 73-13 for *Artemisia* phenophase) under conditions of constant irradiation (1100 microeinsteins/m^2/sec) and varying leaf temperatures. Water potentials (ψ) for each treatment are given adjacent to the appropriate lines. Values are means of 3-4 plants measured, shown ± one standard deviation (A3UCB39).

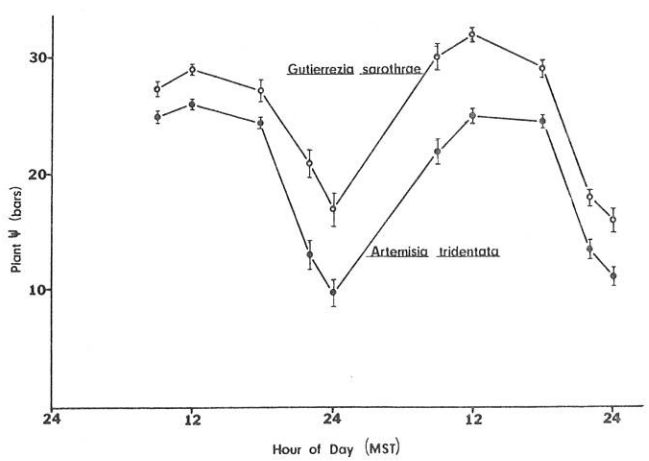


Figure 9. Course of plant water potential (ψ) for two days in August for *Artemisia tridentata* and *Gutierrezia sarothrae* in the field. Values are means of 8-9 plants measured, shown ± one standard deviation.

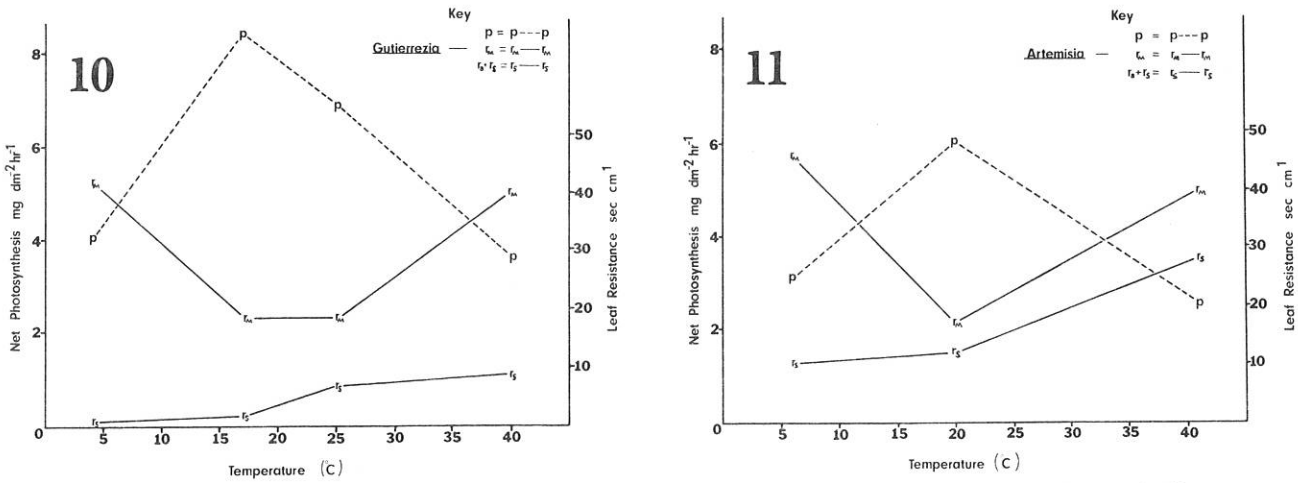


Figure 10-11. Response of net photosynthesis, stomatal diffusion resistance to CO_2 flux ($r'_a + r'_s$) and mesophyll resistance to CO_2 flux (r'_m) for *Gutierrezia sarothrae* (10) and *Artemisia tridentata* (11) to varying leaf temperature under constant irradiation (1400 microeinsteins/m^2/sec). The experiment was carried out on potted plant material with a maximum water potential of -6 bars in the laboratory (A3UCB39).

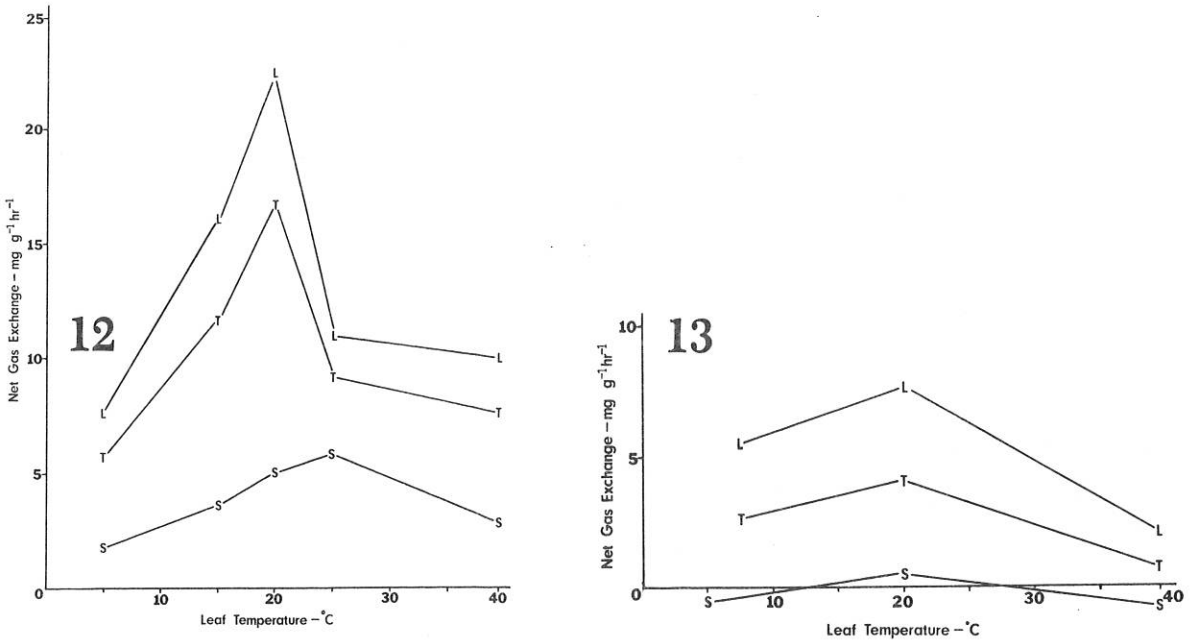
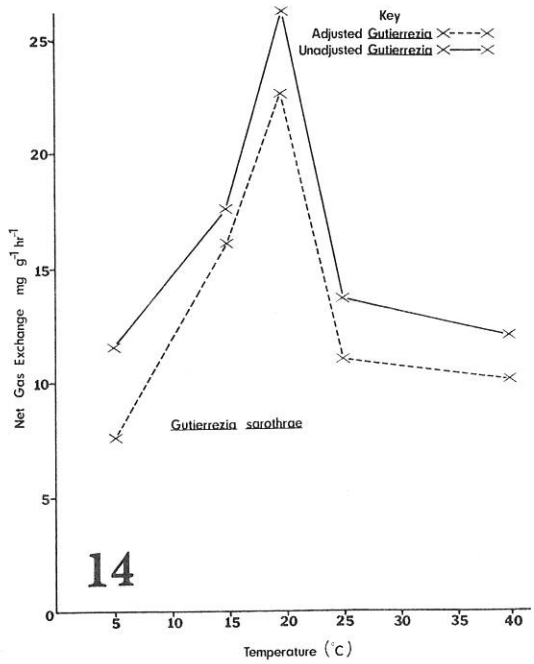
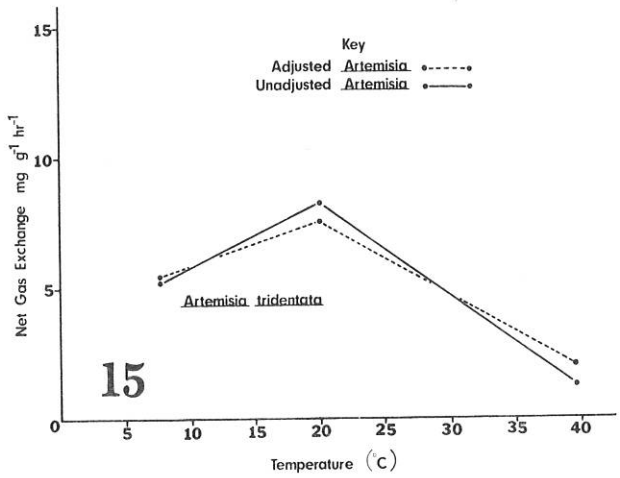


Figure 12-13. Temperature response of net gas exchange of shoots and shoot components for *Gutierrezia sarothrae* (12) and *Artemisia tridentata* (13) under constant irradiation (1100 microeinsteins/m^2/sec). Leaf rates (L—L) are on a per gram leaf dry weight basis; stem rates (S—S) are on a per gram stem dry weight basis; and rates for the entire plant sample (T—T) are on a per gram total shoot dry weight basis. Values are means of 5-8 measurements (shown ± one standard deviation) made on potted plant material during defoliation experiments in the laboratory. Average plant water potential (maximum) was -6.5 bars for Figure 12, -5 bars for Figure 13 (A3UCB39).





Figures 14-15. Apparent differences in net gas exchange rate of *Gutierrezia sarothrae* (14) and *Artemisia tridentata* (15) due to expression of leaf gas exchange rates on a per gram leaf dry weight basis with subtraction of stem gas exchange (adjusted) vs. without subtraction of stem gas exchange (unadjusted). These results were derived from means of 5-8 defoliation experiments carried out on potted plant material in the laboratory under conditions of constant irradiation (1100 microeinsteins/m^2/sec)and varying leaf temperature. Average plant water potential (maximum) was -6.5 bars for *Gutierrezia sarothrae*, and -5 bars for *Artemisia tridentata* .

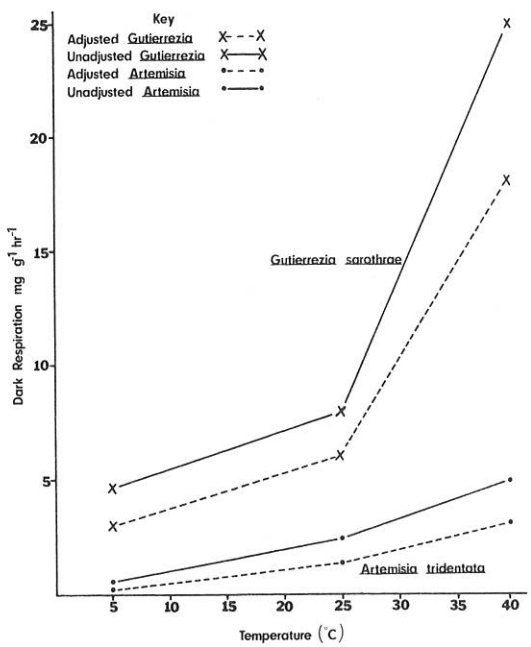


Figure 16. Apparent differences in dark respiration rates of *Gutierrezia sarothrae* and *Artemisia tridentata* due to expression of those rates on a per gram leaf dry weight basis with subtraction of stem respiration (adjusted) vs. without subtraction of stem respiration (unadjusted). These results were derived from means of 5-8 defoliation experiments on potted plant material in the laboratory under conditions of constant irradiation (1100 microeinsteins m^{-2} sec^{-1}) and varying leaf temperatures. Average plant water potential (maximum) of *Gutierrezia sarothrae* was -6.5 bars and of *Artemisia tridentata* was -5 bars.

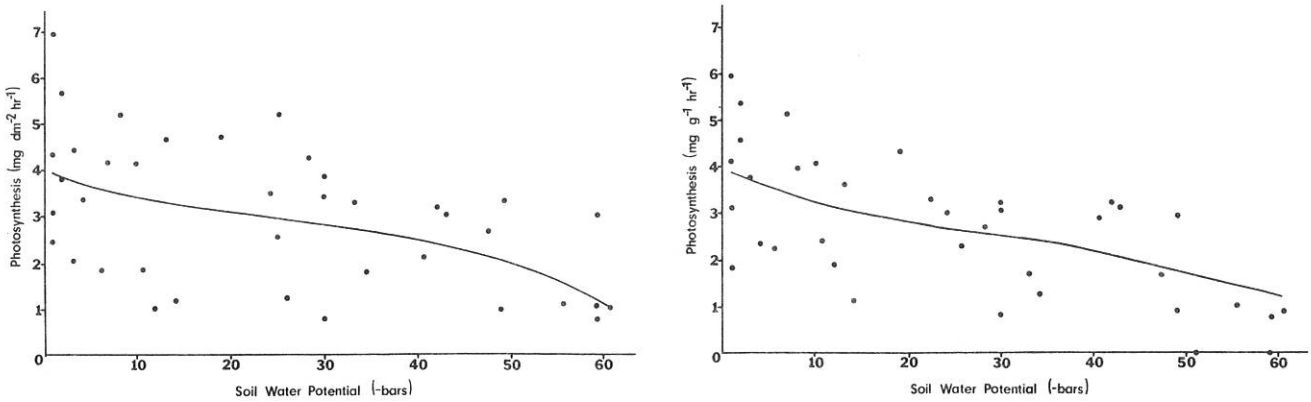


Figure 17. Net photosynthesis of *Atriplex confertifolia* per unit leaf area (above left) and per unit dry weight (above right) as a function of soil water potential at 20 C leaf temperature. A least squares regression curve is also depicted (A3UCB10).

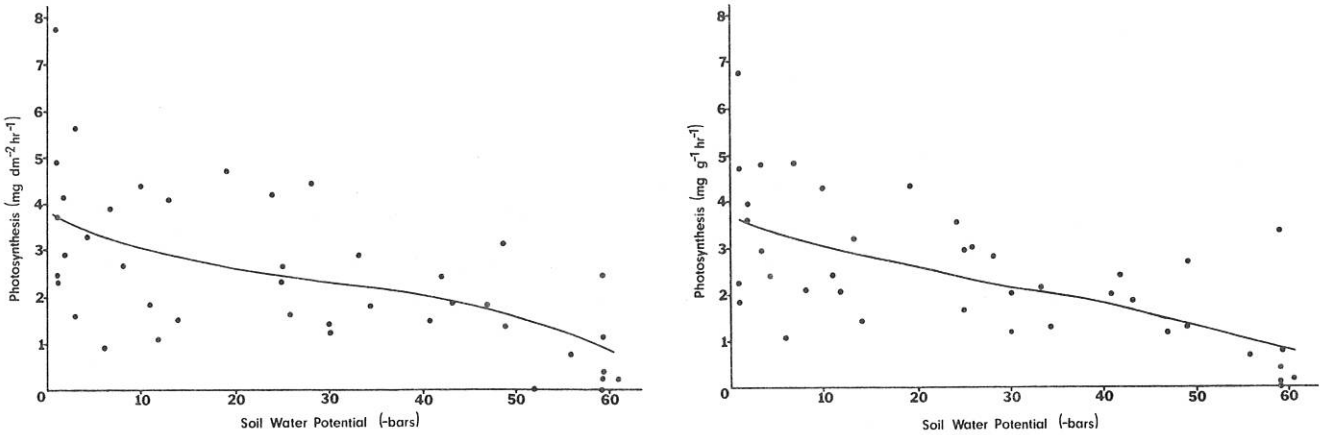


Figure 18. Net photosynthesis of *Atriplex confertifolia* per unit leaf area (above left) and per unit dry weight (above right) as a function of soil water potential at 30 C leaf temperature. A least squares regression curve is also depicted (A3UCB10).

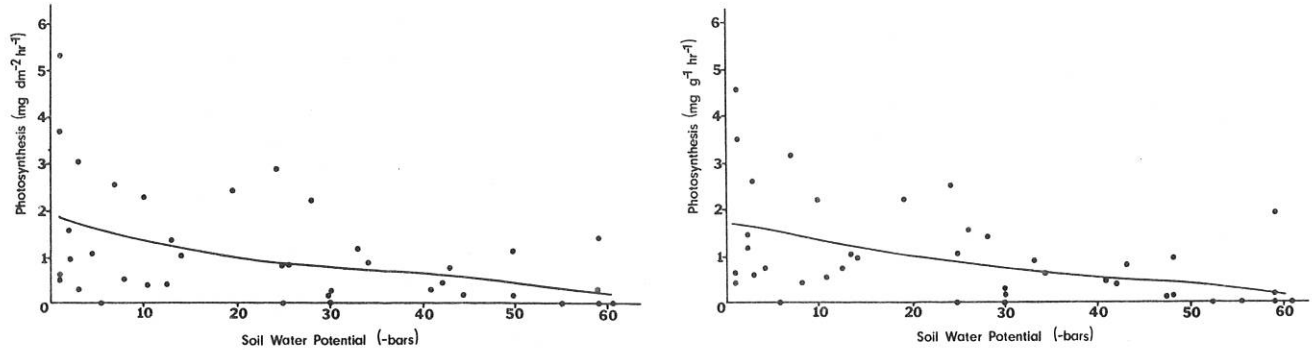


Figure 19. Net photosynthesis of *Atriplex confertifolia* per unit leaf area (above left) and per unit dry weight (above right) as a function of soil water potential at 40 C leaf temperature. A least squares regression curve is also depicted (A3UCB10).

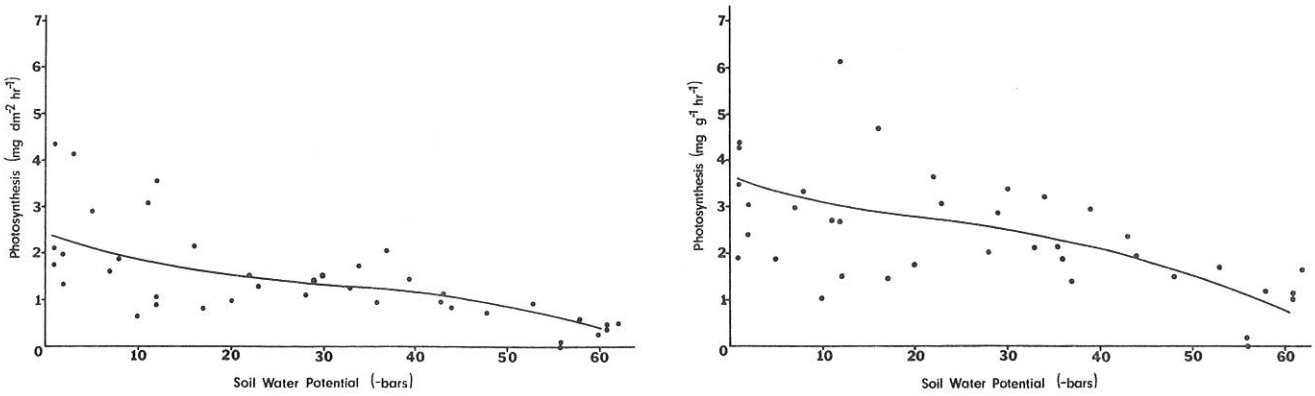


Figure 20. Net photosynthesis of *Ceratoides lanata* per unit leaf area (above left) and per unit dry weight (above right) as a function of soil water potential at 20 C leaf temperature. A least squares regression curve is also depicted (A3UCB10)

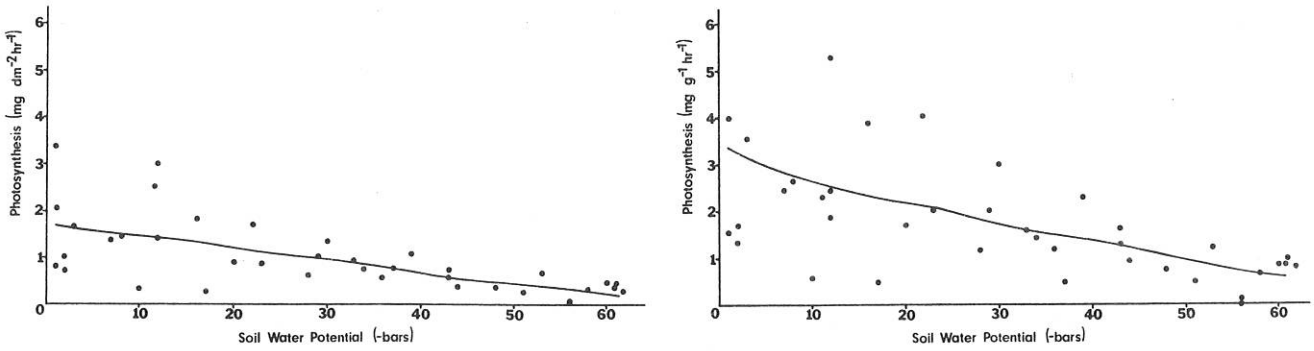


Figure 21. Net photosynthesis of *Ceratoides lanata* per unit leaf area (above left) and per unit dry weight (above right) as a function of soil water potential at 30 C leaf temperature. A least squares regression curve is also depicted (A3UCB10).

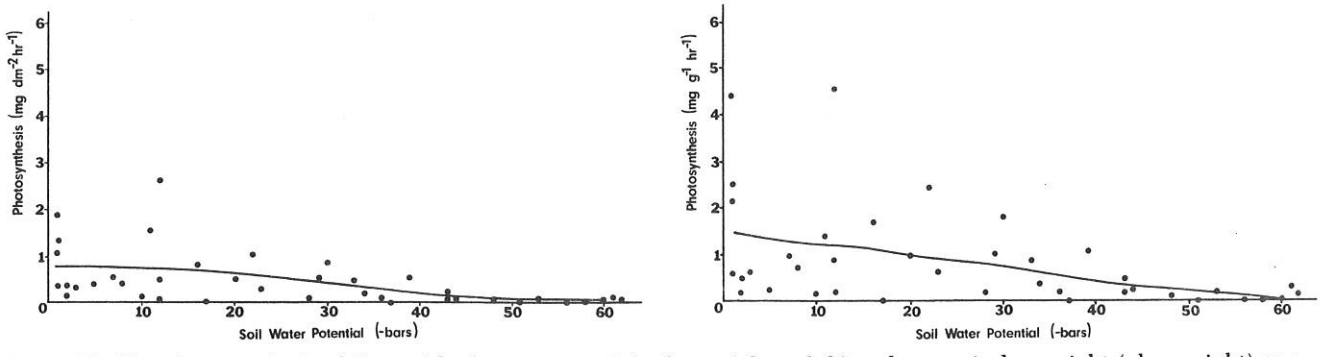


Figure 22. Net photosynthesis of *Ceratoides lanata* per unit leaf area (above left) and per unit dry weight (above right) as a function of soil water potential at 40 C leaf temperature. A least squares regression curve is also depicted (A3UCB10).

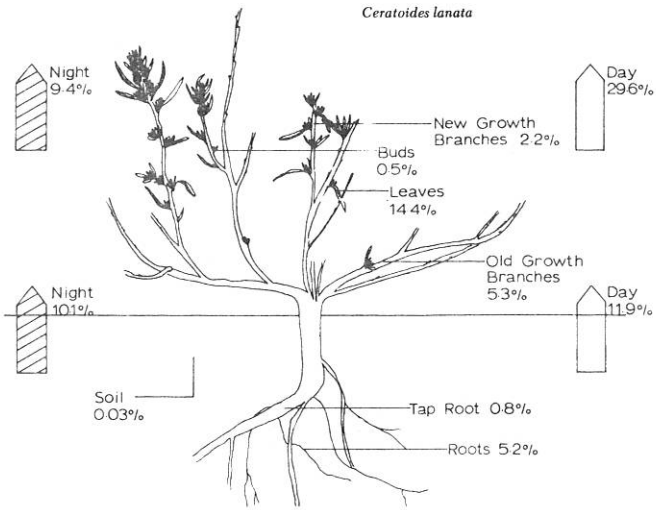


Figure 23. Partitioning of carbon-14 fixed in a closed system over an experimental period of 20 days for a *Ceratoides lanata* plant The plant was exposed to $C^{14}O_2$ for a 4 to 5 hr period on day 1. Of the total carbon-14 fixed, 89% was recovered in this analysis. See Figure 28 for a time representation of $C^{14}O_2$ efflux from the above- and below-ground portions of this plant's system (A3UCB23).

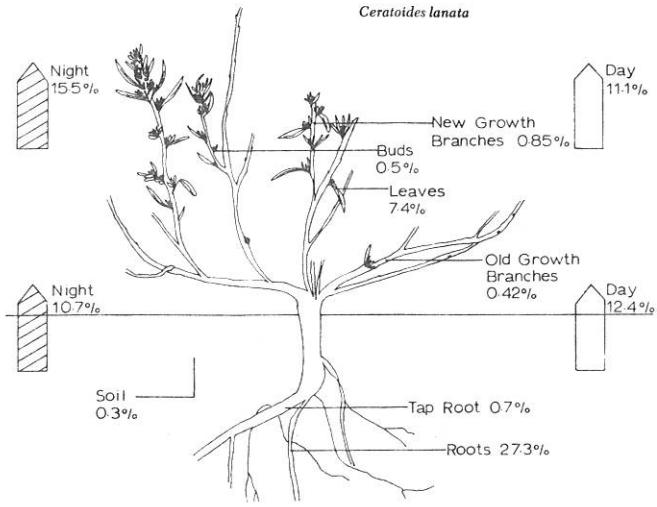


Figure 24. Partitioning of carbon-14 fixed in a closed system over an experimental period of 26 days for a *Ceratoides lanata* plant. The plant was exposed to $C^{14}O_2$ for a 4 to 5 hr period on day 1. Of the total carbon-14 fixed, 84% was recovered in this analysis. See Figure 29 for a time representation of $C^{14}O_2$ efflux from the above- and below-ground portions of this plant's system (A3UCB23).

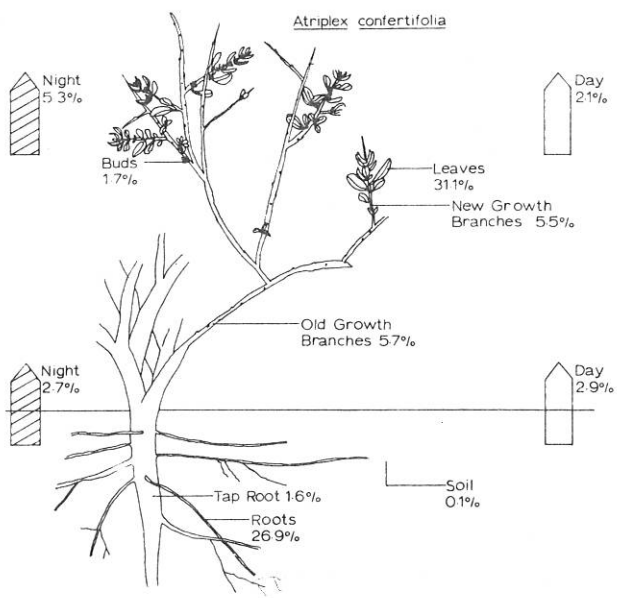


Figure 25. Partitioning of carbon-14 fixed in a closed system over an experimental period of 20 days for an *Atriplex confertifolia* plant. The plant was exposed to $C^{14}O_2$ for a 4 to 5 hr period on day 1. Of the total carbon-14 fixed, 86% was recovered in this analysis. See Figure 30 for a time representation of $C^{14}O_2$ efflux from the above- and below-ground portions of this plant's system (A3UCB23).

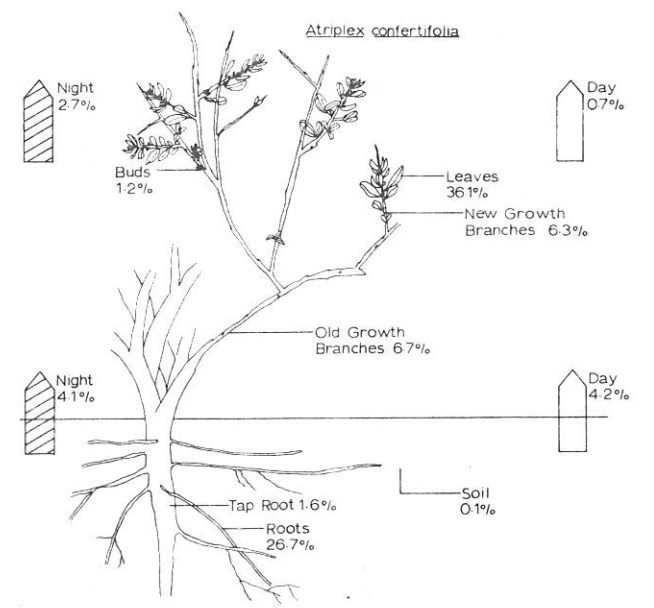


Figure 26. Partitioning of carbon-14 fixed in a closed system over an experimental period of 18 days for an *Atriplex confertifolia* plant. The plant was exposed to $C^{14}O_2$ for a 4 to 5 hr period on day 1. Of the total carbon-14 fixed, 91% was recovered in this analysis. See Figure 31 for a time representation of $C^{14}O_2$ efflux from the above- and below-ground portions of this plant's system (A3UCB23).

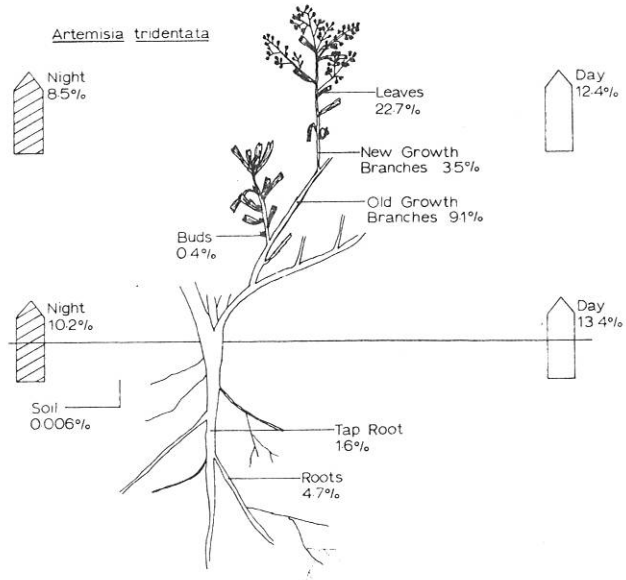
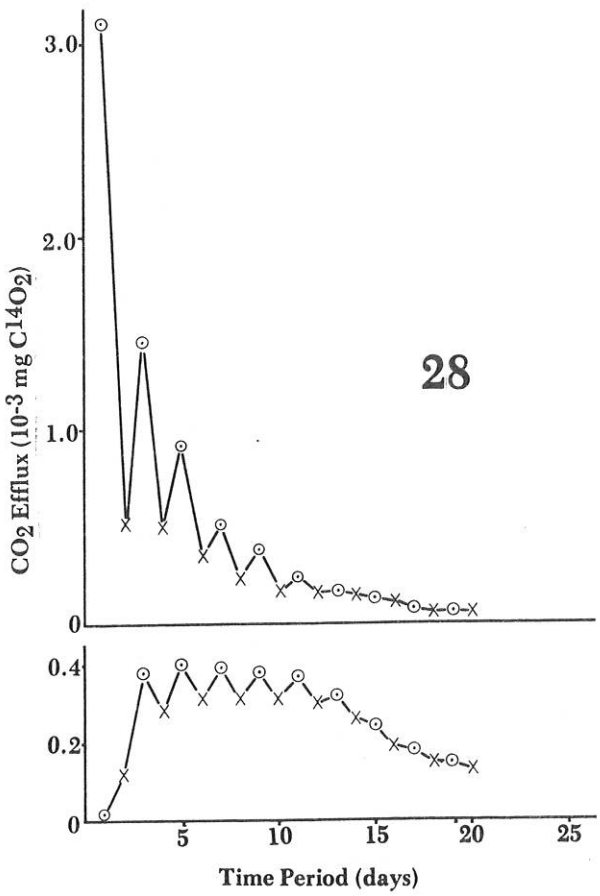
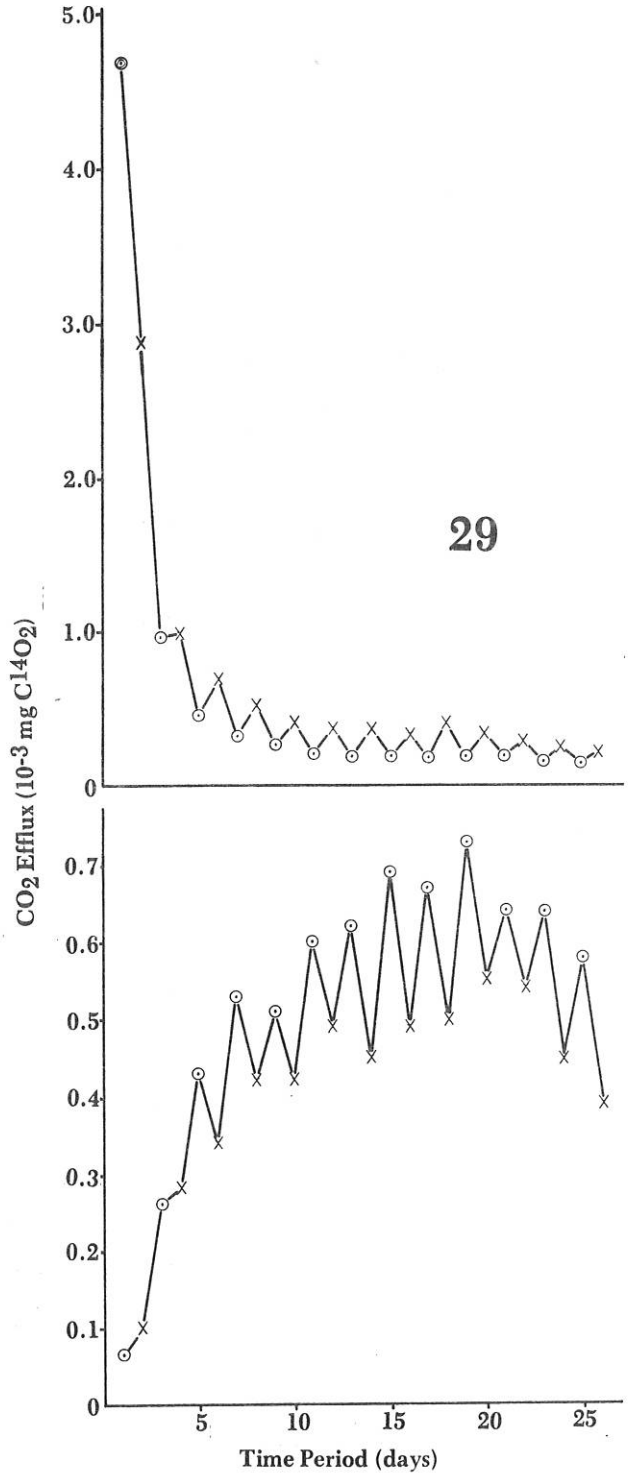
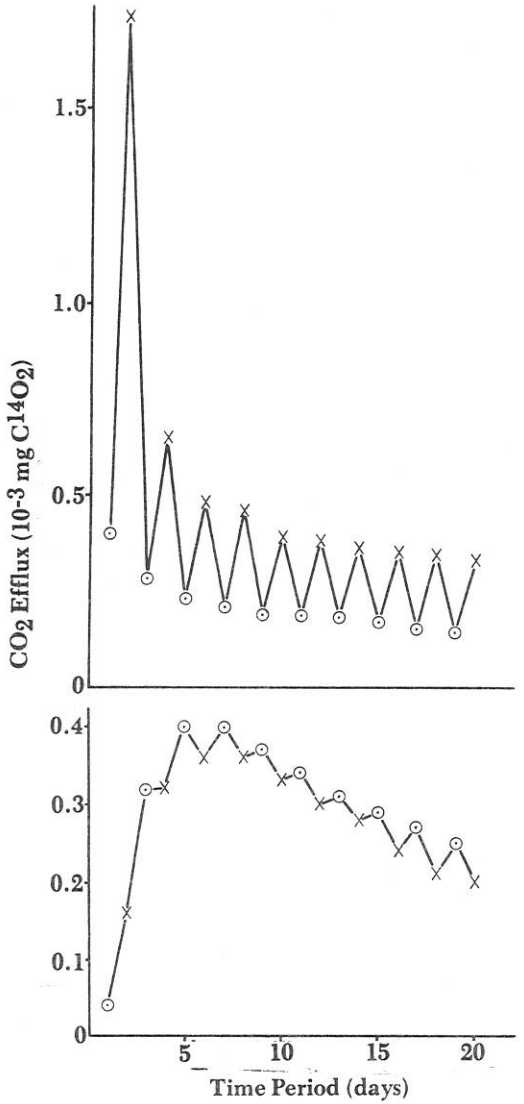


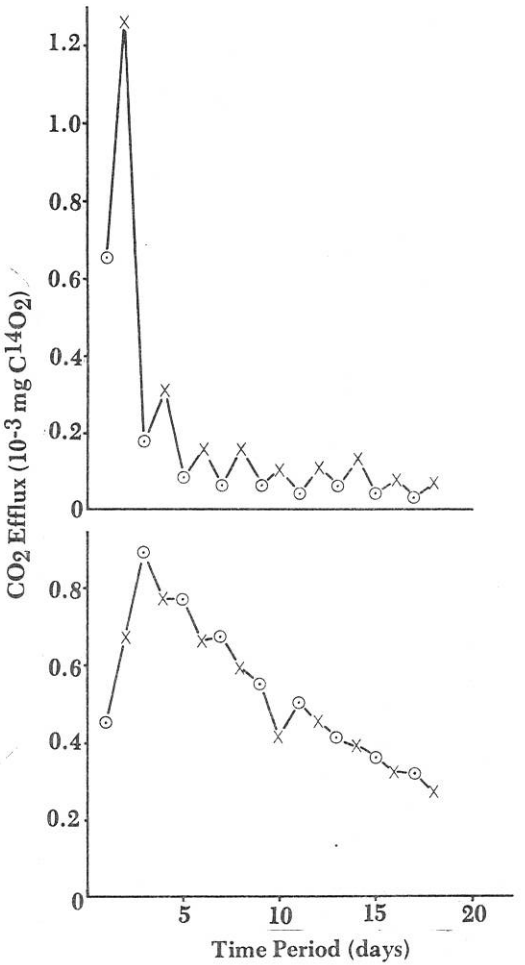
Figure 27. Partitioning of carbon-14 fixed in a closed system over an experimental period of 18 days for an *Artemisia tridentata* plant. The plant was exposed to $C^{14}O_2$ for a 4 to 5 hr period on day 1. Of the total carbon-14 fixed, 87 % was recovered in this analysis. See Figure 32 for a time representation of $C^{14}O_2$ efflux from the above- and below-ground portions of this plant's system (A3UCB23).





Figures 28-29. Efflux of $C^{14}O_2$ from the above- and below-ground portions of a *Ceratoides lanata* plant in a closed system. Efflux of $C^{14}O_2$ is represented for 12-hr periods with X denoting the nighttime efflux and O denoting daytime efflux (A3UCB23). The photoperiod was 12 hr with a night air temperature of 15 C and a soil temperature during the day of 24 C. In Figure 28 (left) the day air temperature was 30 C and night soil temperature was 22 C. In Figure 29, the day air temperature was 25 C and night soil temperature was 21 C.





Figures 30-31. Efflux of $C^{14}O_2$ from the above- and below-ground portions of an *Atriplex confertifolia* plant in a closed system. Efflux of $C^{14}O_2$ is represented for 12-hr periods with X denoting the nighttime efflux and O denoting daytime efflux (A3UCB23). The photoperiod was 12 hr. In Figure 30 (left) there was a night air temperature of 20 C, a day air temperature of 30 C, a night soil temperature of 21 C, and day soil temperature of 25 C. In Fig. 31, there was a night air temperature of 15 C, a day air temperature of 25 C, a night soil temperature of 21 C, and a day soil temperature of 23 C.

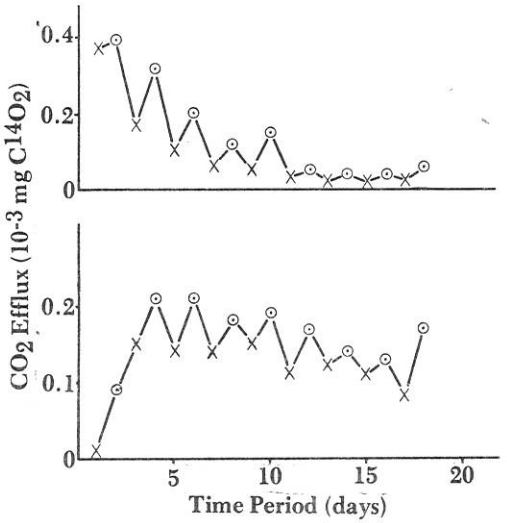


Figure 32. Efflux of $C^{14}O_2$ from the above- and below-ground portions of an *Artemisia tridentata* plant in a closed system. Efflux of $C^{14}O_2$ is represented for 12-hr periods with X denoting the nighttime efflux and O denoting daytime efflux (A3UCB23). The photoperiod was 12 hr with a night air temperature of 15 C, a day air temperature of 30 C, a night soil temperature of 22 C, and a soil temperature during the day of 24 C.

Table 1. Partitioning of photosynthates to plant parts -- *Atriplex confertifolia* (A3UCB20)

Shoots	April			July			September			September April Treatment			September July Treatment		
	Plant 1	Plant 2	Plant 3	Plant 1	Plant 2	Plant 3	Plant 1	Plant 2	Plant 3	Plant 1	Plant 2	Plant 3	Plant 1	Plant 2	Plant 3
	DPM/mg dry wt.			DPM/mg dry wt.			DPM/mg dry wt.			DPM/mg dry wt.			DPM/mg dry wt.		
Apical new buds	18552	19739	21035												
New expanding leaves	13470	13709	16078												
Mature leaves, previous year	2073	2368	2798												
New branches, current year	11200	10315	12640	1699	2060	1763	116	115	149	871	619	627	1123	1407	1220
Secondary branches, previous year	713	872	1022	824	620	797	96	76	95	412	328	426	549	707	590
Primary branches, previous year	594	560	768	777	609	526	60	49	51	365	208	290	482	509	500
Main stem and crown	321	201	563	421	386	220	35	41	38	177	205	200	218	258	190
Flowers and fruits (female plant)				1319	1236	1318	139	146	116	98	123	107	635	806	666
Axilary vegetat. buds				1028	1161	988	169	203	171	214	179	149	478	518	440
Fully expanded leaves, current year				598	674	649	153	156	169	420	371	360	492	587	490
Spines	145	121	164												
Roots															
Main tap root	390	470	401	201	777	402	19	18	16	101	119	75	237	473	
Lateral 5-10 mm diam.	460	580	480	120	871	202	15	19	16	145	161	46			
Lateral 2-5 mm diam.	147	120	520	230	944	462	26	18	14	99	89	90	226	187	
Lateral 1-2 mm diam.	171	127	120	343	1377	621	20	45	20	88	101	66		206	
Lateral .2-1 mm diam.	277	307	601	203		176		255		138	163	140	381	256	
Lateral less .2 mm diam.	220	341	408		956	880				150	181				

Table 2. Partitioning of photosynthates to plant parts -- *Ceratoides lanata* (A3UCB20)

Shoots	April			July			September			September April Treatment			September July Treatment		
	Plant 1	Plant 2	Plant 3	Plant 1	Plant 2	Plant 3	Plant 1	Plant 2	Plant 3	Plant 1	Plant 2	Plant 3	Plant 1	Plant 2	Plant 3
	DPM/mg dry wt.			DPM/mg dry wt.			DPM/mg dry wt.			DPM/mg dry wt.			DPM/mg dry wt.		
Upper buds	4450	4610	4517				206	214	227	21	20	18	686	643	702
Lower axilary new buds	4207	5172	4218												
Mature leaves, previous year	1107	971	878												
Tertiary branches (holding buds)	209	323	226	1770	1966	2120	91	79	82	71	67	66	726	691	696
Secondary branches	152	144	135	1662	1657	1447	63	76	69	69	60	42	575	456	471
Primary branches	56	203	48	743	952	485	78	87	57	31	19	26	430	334	388
Main stem and crown	27	122	61	455	543	413	56	39	33	27	25	31	161	198	157
Flowers (female)				975	1048	934									
Flowers (male)				440	532	528									
Expanded leaves, current year				970	853	1041	194	194	205	28	20	27	395	341	401
Vegetative axilary buds				1443	1580	1645	219	196	187	26	25	30	777	846	860
New branches, current year				1966	1491	1890	166	188	186	66	54	51	898	861	866
Roots															
Main tap root	65	14	36	450	495	154	40	32	51		19		178	101	151
Lateral 5-10 diam.				378	514		52		41						
Lateral 2-5 mm diam.	67	25	32	496	432	385	91	70	96	21	28	17	205	222	121
Lateral 1-2 mm diam.	45	29	62	282	593	351	73	77	81	17	33	27	249	146	271
Lateral .2-1 mm diam.	69	54	86	548	614	752	79	75	97	24	36	22	313	341	370
Lateral less .2 mm diam.	21	39	21	546	714	1086	67	62	27	43	65	71	344	521	446

Table 3. Average percent partitioning of photosynthates to plant parts - *Atriplex confertifolia* (A3UCB20)

	April %	July %	September %	September April Treatment %	September July Treatment %
Shoots					
Apical new buds	38.1				
New expanding leaves	27.8				
Mature leaves, previous year	4.6				
New branches, current year	21.9	18.7	27.7	23.6	23.3
Secondary branches, previous year	1.7	7.6	6.5	13.0	11.5
Primary branches, previous year	1.2	6.5	3.9	9.6	9.2
Main stem and crown	0.7	3.5	2.8	6.6	4.1
Flowers and fruits (female plants)		13.1	9.8	3.6	13.1
Axilary vegetative buds		10.8	13.2	6.1	8.9
Fully expanded leaves, current year		6.5	11.6	12.9	9.7
Spines	0.3				
	(96.3)	(66.7)	(75.5)	(75.4)	(79.8)
Roots					
Main tap root	0.8	4.6	1.3	3.3	6.6
Lateral 5-10 mm diam.	0.8	4.0	1.2	3.9	
Lateral 2-5 mm diam.	0.5	5.5	1.4	3.1	3.8
Lateral 1-2 mm diam.	0.3	7.9	2.0	3.9	3.8
Lateral .2-1 mm diam.	0.7	1.9	18.6	4.9	5.9
Lateral less .2 mm diam.	0.6	9.3		5.5	
	(3.7)	(33.3)	(24.5)	(24.6)	(20.2)

Table 4. Average percent partitioning of photosynthates to plant parts -- *Ceratoides lanata* (A3UCB20)

	April %	July %	September %	September April Treatment %	September July Treatment %
Shoots					
Upper new buds	41.8		14.8	4.3	11.2
Lower axilary new buds	41.8				
Mature leaves, previous year	9.1				
Tertiary branches (holding buds)	2.3	14.4	5.8	14.8	11.7
Secondary branches	1.3	11.7	4.8	12.4	8.3
Primary branches	0.9	5.3	5.1	5.4	6.4
Main stem and crown	0.7	3.2	2.9	6.1	5.7
Flowers (female)		7.2			
Flowers (male)		3.9			
Expanded leaves, current year		7.0	13.6	5.4	6.3
Vegetative axilary buds		11.4	13.9	5.8	13.7
New branches, current year		13.1	12.4	12.4	14.4
	(97.9)	(77.2)	(73.3)	(66.6)	(77.7)
Roots					
Main tap root	0.4	2.7	2.8	4.1	2.3
Lateral 5-10 mm diam.		3.3	3.2		
Lateral 2-5 mm diam.	0.4	3.2	6.0	4.8	3.0
Lateral 1-2 mm diam.	0.4	3.0	5.3	5.6	3.7
Lateral .2-1 mm diam.	0.6	4.8	5.8	5.9	5.6
Lateral less .2 mm diam.	0.3	5.8	3.6	13.0	7.7
	(2.1)	(22.8)	(26.7)	(33.4)	(22.3)

Table 5. Total allocation photosynthates to shoots and roots -- relative values on land area bases -- *Atriplex confertifolia*-dominated community

Date	Plant component	Biomass kg/ha	Biomass mg/dm^2	DPM mg^{-1} dry wt.	DPM dm^{-2}	Total DPM dm^{-2} plant component	Percent allocation
July	New shoot growth	1,542	1,542	1,200.0	1,850,400	1,850,400	63.3
	Old shoot growth	1,214	1,214	442.0	536,588	536,588	18.3
	Root system						
	5-30[1]	9,224	9,224	33.0	304,392		
	30-50	5,469	5,469	21.3	117,490		
	50-70	4,010	4,010	29.3	117,493	538,375	18.4
September	New shoot growth	1,163	1,163	98.0	113,974	113,974	51.4
	Old shoot growth	1,201	1,201	47.0	56,447	56,447	25.4
	Root system						
	5-30	9,224	9,224	2.5	23.060		
	30-50	5,469	5,469	3.5	19,142		
	50-70	4,010	4,010	2.3	9,223	51,425	23.2
April-Sept.	New shoot growth	1,163	1,163	308.0	358,204	358,204	36.5
	Old shoot growth	1,201	1,201	233.0	279,833	279,833	28.5
	Root system						
	5-30	9,224	9,224	21.5	198,316		
	30-50	5,469	5,469	19.0	103,911		
	50-70	4,010	4,010	10.0	40,100	342,327	35.0
July-Sept.	New shoot growth	1,163	1,163	759.0	882,717	882,717	49.7
	Old shoot growth	1,201	1,201	314.0	377,114	377,114	21.2
	Root system						
	5-30	9,224	9,224	39.3	362,503		
	30-50	5,469	5,469	15.3	83,676		
	50-70	4,010	4,010	17.5	70,175	516,354	29.1

1 Depth in centimeters

Table 6. Total allocation of photosynthates to shoots and roots -- relative values on land area bases -- *Ceratoides lanata*-dominated community

Date	Plant component	Biomass kg/ha	Biomass mg/dm^2	DPM mg^{-1} dry wt.	DPM dm^{-2}	Total DPM dm^{-2} plant component	Percent allocation
July	New shoot growth	638	638	1,017.0	648,846	648,846	42.0
	Old shoot growth	823	823	359.0	295,457	295,457	19.1
	Root system						
	5-30[1]	7,103	7,103	49.5	351,598		
	30-50	5,176	5,176	25.0	129,400		
	50-70	3,807	3,807	31.5	119,920	600,918	38.9
September	New shoot growth	548	548	131.0	71,788	71,788	41.9
	Old shoot growth	818	818	35.0	28,630	28,630	16.7
	Root system						
	5-30	7,103	7,103	4.8	34,094		
	30-50	5,176	5,176	3.8	19,669		
	50-70	3,807	3,807	4.5	17,131	70,894	41.4
April-Sept.	New shoot growth	548	548	68.0	37,264	37,264	13.9
	Old shoot growth	818	818	68.0	55,624	55,624	20.8
	Root systems						
	5-30	7,103	7,103	15.5	110,097		
	30-50	5,176	5,176	8.0	41,408		
	50-70	3,807	3,807	6.0	22,842	174,347	65.3
July-Sept.	New shoot growth	548	548	479.0	262,492	262,492	32.3
	Old shoot growth	818	818	310.0	253,580	253,580	31.9
	Root systems						
	5-30	7,103	7,103	12.3	87,367		
	30-50	5,176	5,176	30.5	157,868		
	50-70	3,807	3,807	13.5	51,395	296,630	36.5

1 Depth in centimeters

refers to both live and dead portions. These translocation values indicate the concentration of labeled carbon in various plant parts. This does not, however, yield information as to the total amount of carbon per unit ground area allocated to various plant parts. This has not been done because of the magnitude of the task involved in determining biomass per unit ground area of individual plant parts such as spines, buds, twigs of various age, etc. Therefore, allocation of carbon at the community level has also been assessed on the basis of shoots (current year's growth versus that of previous years) and underground plant parts. In this manner, too, biomass estimates in these communities could be obtained at a suficient level of sampling intensity to estimate the mean within ± 15% coefficient of variation.

Allocation of Carbon at Community Level

The allocation of carbon at the community level for these stands dominated by *Atriplex confertifoli* and *Ceratoides lanata* are given in Tables 5 and 6. This is derived simply from a proportion of carbon-14 translocated to various plant parts multiplied by the amount of biomass in these components of the community. Biomass values are also given in these tables. These are based on harvests of twelve 4.8-m^2 plots in the *Atriplex* community and twelve 1.2-m^2 plots in the *Ceratoides* community. For root biomass, 8 to 12 core samples were taken in each plot. The number in the total community varied with sampling variance. The number of cores was increased until the mean was estimated within ± 15% coefficient of variation. As was the case with the translocation experiments, underground biomass includes both live and dead components. During 1973 a series of techniques was tried in order to obtain a method of suitably separating live from dead unerground material. For carbon allocation and biomass studies such as have been carried out here, the method would need to be applicable for large amounts of material. One technique involving a separation of material by differential density in methanol solutions appears to be very promising and will be pursued further in 1974. Hopefully, future determinations of allocation, translocation and underground turnover can be based purely on living material.

Below-Ground Productivity

Even with an accurate method of determining living biomass in natural plant communities, there is little indication of underground productivity, or what might be termed annual below-ground turnover rates. With desert shrub communities such as those in Curlew Valley where a high proportion of the plant systems are underground, the importance of assessing turnover rates in the overall carbon balance of the communities becomes quite apparent. There exists no single, truly satisfactory technique for determining these underground turnover rates in a natural undisturbed community. The root observation chambers discussed later, although valuable for determining the timing and extent of root activity, do not permit a quantitative indication of underground biomass turnover. Three independent techniques have been tried in this study to gain some estimate of underground turnover rates. Each has certain assumptions and definite drawbacks. These will be discussed in greater detail in the Discussion section.

Soil CO_2 Efflux

For a community which is in steady state, the yearly amount of carbon-dioxide efflux from the soil surface should reflect the annual quatity of carbon placed underground by primary producers in that system along with CO_2 efflux resulting from shoot litter decomposition in the soil. The trend of carbon dioxide efflux from the soil surface is shown in Figures 33 through 35 for the *Atriplex*, *Ceratoides* and *Artemisia* communities (A3UCB25). Except at the early part of the season, effluxes from the ground surface between or immediately beneath shrub canopies are very similar.

Reinvasion of Soil Cores

A second estimate of below-ground turnover has involved measures of the reinvasion of roots into root-free soil cores. Soil cores with roots removed in early 1972 and then replaced were again excavated in September, 1973. As was outlined in the Methods section, this was carried out in two modes, with and without the nylon sock surrounding the replaced soil. The biomass of roots reinvading the soil cores is given in Table 7 along with comparative biomass values taken from undisturbed soil cores in these three communities (A3UCB26).

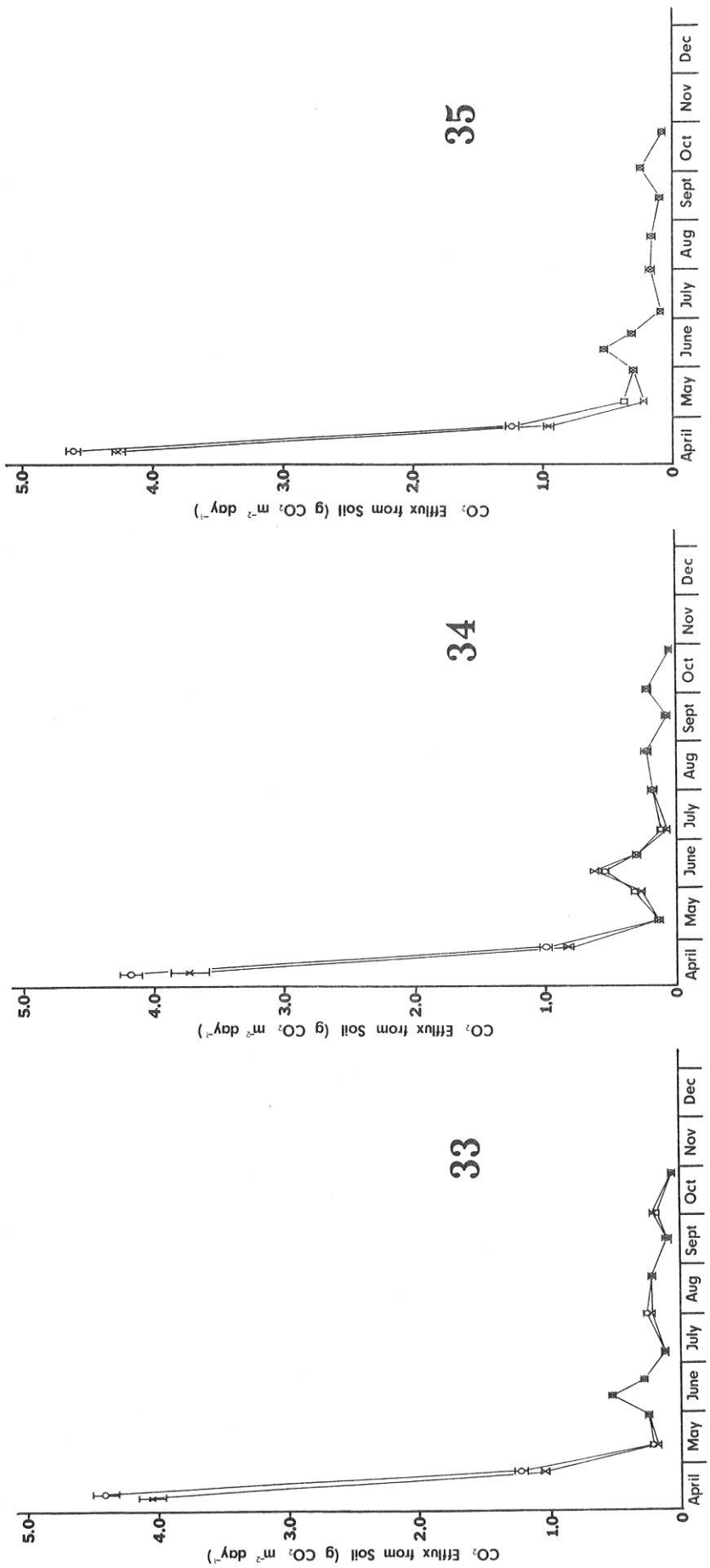
Turnover Based on Dilution Technique

The third estimate of underground turnover rates was based upon the new C^{14}/C^{12} dilution technique explained in the Methods section. Values for C^{14}/C^{12} dilution in the *Atriplex* and *Ceratoides* communities between April and September are shown in Table 8 (A3UCB27). These render turnover factors which are also in this table. This then represents the carbon replacement, or turnover, in the root system between April and September.

A comparison of the productivity values derived from each of these three methods will be depicted in the Discussion section along with a discussion of the errors and assumptions connected with each of them.

Foliage Area Indices

Foliage area index values for 16 plots in the *Ceratoides* community indicate a mean value of 0.54 with a standard deviation of ± 0.19. These values were derived by the inclined point frame technique in early August after the annual shoot growth had ceased. For *Atriplex confertifolia*, as was explained in the Methods section, it was only possible to do intensive foliage-area index determinations for four individual shrubs. These values yielded a mean foliage area index of 1.5 with a standard deviation of ± 0.9. From a series of 20 photographed plots in the *Atriplex* community, a mean percent canopy coverage of 36% ± 12.8% standard deviation was derived. Using these extremely crude indices of foliage-area index for the crown projection of *Atriplex* of 1.5, and the mean percent crown projection area coverage in the community of 36%, a foliage area index value for the



Figures 33-35. Carbon dioxide efflux from the soil surface in three shrub communities in 1973 (Fig. 33, *Atriplex confertifolia;* Fig. 34, *Ceratoides lanata;* Fig. 35, *Artemisia tridentata*). The symbol O denotes efflux from soils under the crown projections of the shrubs. The symbol X denotes efflux from soils between shrubs. The standard errors are indicated by vertical bars (A3UCB25).

Table 7. Biomass of roots reinvading soil cores between April 1, 1972, and September 17, 1973 (A3UCB26)

Species	Depth (cm)	Mean dry wt. of roots which would not pass through a 1 mm sieve (g)	Mean dry wt. of roots which passed through a large sieve but not small 0.5 mm sieve (g)	Mean dry wt. of total sample (g)	Standard error of total sample (g)	Comparative biomass in undisturbed soil cores harvested September 17, 1973 Mean	Standard error
Atriplex confertifolia with nylon sock	0-30	1.49	0.59	2.08	0.296		
	30-60	0.87	0.31	1.18	0.123		
Atriplex confertifolia without nylon sock	0-30	4.49	2.14	6.63	0.67	3.38	0.28
	30-60	1.91	0.75	2.66	.294	2.87	0.24
Artemisia tridentata with nylon sock	0-30	1.62	0.69	2.31	.213		
	30-60	1.20	0.92	2.13	0.26		
Artemisia tridentata without nylon sock	0-30	3.27	1.69	4.96	.37	5.88	0.12
	30-60	1.70	1.60	3.30	.41	5.07	0.22
Ceratoides lanata with nylon sock	0-30	1.07	0.46	1.54	.11		
	30-60	1.21	0.36	1.57	.15		
Ceratoides lanata without nylon sock	0-30	2.09	1.00	3.09	.21	4.21	0.35
	30-60	2.47	0.83	3.30	.16	6.41	0.33

Table 8. Relative $^{14}C/^{12}C$ ratios in cell wall tissues of root in the *Atriplex confertifolia*- and *Ceratoides lanata*-dominated communities (A3UCB27)

Date	Species	Depth (cm)	Type of Roots	Mean Relative $^{14}C/^{12}C$ Ratios	Standard Error	Percent cell wall tissue	Turnover Coefficients
5-8-73	*Atriplex confertifolia*	0-25	Lateral	34.2	± 1.5	53	
		25-50	"	30.9	± 1.9	49	
		50-75	"	26.1	± 1.6	52	
9-18-73		0-25	"	16.8	± 1.8	52	1.07
		25-50	"	9.1	± 0.6	47	2.54
		50-75	"	3.4	± 0.3	56	6.13
5-8-73			Tap Root	41.3	± 2.0	43	
9-18-73			"	35.2	± 1.7	46	0.10
4-26-73	*Ceratoides lanata*	0-25	Lateral	10.1	± 0.6	51	
		25-50	"	7.6	± 0.4	49	
		50-75	"	5.6	± 0.3	56	
9-18-73		0-25	"	5.8	± 0.4	51	0.74
		25-50	"	5.8	± 0.3	52	0.23
		50-75	"	4.4	± 0.3	52	0.37
4-26-73			Tap Root	13.1	± 0.9	41	
9-18-73			"	9.2	± 0.6	42	0.39

Table 9. Relative growth rate for the root growth of *Atriplex confertifolia* --1973 season

Depth	April 19 May 1	May 1 May 10	May 10 May 22	May 22 May 31	May 31 June 19	June 19 July 17	July 17 Aug. 1	Aug. 1 Aug. 16	Aug. 16 Aug. 30	Aug. 30 Sept. 10	Sept.10 Nov. 14
					(cm cm^{-1} day^{-1})						
0-10	0.022	0.070	$3.606X10^{-3}$	$2.012X10^{-3}$	$2.550X10^{-3}$	$1.912X10^{-3}$		$2.769X10^{-4}$			
10-20	0.052	0.116	0.036	0.127	$2.517X10^{-3}$	$3.254X10^{-3}$	$6.153X10^{-3}$	$1.871X10^{-3}$			
20-30			0.254	0.045	0.166	$9.578X10^{-3}$	$3.338X10^{-3}$			$6.591X10^{-5}$	
30-40		0.126	0.143	0.061	0.021	$7.666X10^{-3}$	$7.420X10^{-4}$			$3.464X10^{-4}$	$9.463X10^{-5}$
40-50			0.093	0.742	0.023	0.121	$3.140X10^{-3}$		$6.953X10^{-4}$	$2.014X10^{-4}$	
Total	0.033	0.110	0.056	0.035	0.013	$7.434X10^{-3}$	$2.881X10^{-3}$	$4.437X10^{-4}$	$4.252X10^{-4}$	$3.888X10^{-4}$	$2.887X10^{-5}$

Table 10. Relative growth rates for the root growth of *Ceratoides lanata* -- 1973 season

Depth	April 9 May 10	May 10 May 22	May 22 May 31	May 31 June 19	June 19 July 17	July 17 Aug. 1	Aug. 1 Aug. 16	Aug. 16 Aug. 30	Aug. 30 Sept. 10
					(cm cm^{-1} day^{-1})				
0-10		0.151	$9.112X10^{-3}$	0.031	$3.052X10^{-4}$				$8.070X10^{-4}$
10-20	0.034	0.103	0.185	0.172	$4.069X10^{-3}$	$5.025X10^{-4}$	$2.690X10^{-4}$		
20-30	0.067	0.097	0.079	0.011	0.010	$1.286X10^{-4}$	$1.699X10^{-3}$	$8.935X10^{-4}$	
30-40	0.030	0.082	0.041	0.014	0.012	$4.859X10^{-3}$	$6.625X10^{-4}$	$3.550X10^{-3}$	
40-50	0.014	0.175	$5.545X10^{-3}$	0.011	0.031	0.149	$4.550X10^{-3}$	$2.844X10^{-3}$	$1.212X10^{-3}$
Total	0.0362	0.110	0.0338	0.0155	0.012	$5.728X10^{-3}$	$1.908X10^{-3}$	$1.974X10^{-3}$	$6.520X10^{-4}$

Table 11. Relative growth rates for the root growth of *Artemisia tridentata* -- 1973 season

Depth	March 23 April 9	April 9 April 19	April 19 May 1	May 1 May 10	May 10 May 22	May 22 May 31	May 31 June 19	June 19 July 17	July 17 Aug. 1	Aug. 1 Aug. 16	Aug. 16 Aug. 30	Aug. 30 Sept. 10	Sept. 10 Sept. 27	Sept. 27 Oct.10
						(cm cm^{-1} day^{-1})								
0-10		0.101	0.051	0.045	0.078	$8.991X10^{-3}$	$2.119X10^{-3}$	$4.751X10^{-3}$	$5.096X10^{-4}$	$7.349X10^{-5}$		$5.909X10^{-4}$	$1.075X10^{-2}$	
10-20	0.173	0.068	0.050	0.043	0.028	$3.538X10^{-3}$	$3.061X10^{-3}$	$2.318X10^{-3}$	$1.200X10^{-4}$	$1.198X10^{-4}$		$6.281X10^{-5}$		
20-30		0.070	0.084	0.028	0.030	$7.802X10^{-3}$	$4.081X10^{-3}$	$1.700X10^{-3}$	$6.170X10^{-4}$	$1.866X10^{-4}$		$1.435X10^{-4}$		
30-40		0.031	0.234	0.060	0.071	0.036	0.019	$7.696X10^{-3}$	$1.016X10^{-3}$	$9.316X10^{-4}$		$3.233X10^{-4}$		
40-50				0.180	0.112	0.058	0.029	0.014	$2.293X10^{-3}$	$2.545X10^{-3}$	$3.064X10^{-4}$	$4.160X10^{-4}$	$3.214X10^{-4}$	$5.106X10^{-4}$
Total	0.213	0.072	0.0716	0.0415	0.043	0.014	$8.820X10^{-3}$	$5.291X10^{-3}$	$7.874X10^{-4}$	$8.245X10^{-4}$	$5.342X10^{-5}$	$3.633X10^{-4}$	$1.250X10^{-4}$	2.160X10-4

community of 0.54 was derived. This estimate for the *Atriplex* community is considered to be extremely crude and probably quite conservative.

Root Observation Chambers

The extent and timing of root growth activity during the season for *Atriplex confertifolia*, *Ceratoides lanata* and *Artemisia tridentata* are represented in Tables 9 to 11. In each case this represents approximately one-fourth of the total observations. The remainder will be reported at the end of 1974. The quantities of relative root growth represented in Tables 9 to 11 are calculated using the classic relative growth rate formula:

$$RGR = \frac{\ln R_2 - \ln R_1}{t_2 - t_1}$$

where the initial root quantity at each time period is taken in total cm of roots from the current season's growth, R_1, and similarly the quantity at the end of each time period, R_2. The time period in days is calculated as t_2-t_1. The relative growth rate units then are in cm growth per cm of current year's root mass per day. This then yields a relative index of the extent of root growth activity at various depths in the soil profile for various times of the year.

DISCUSSION

In Figure 1, rates of net photosynthesis for *Gutierrezia sarothrae* under conditions of constant irradiation and variable temperature in phenological stages 3 through 7 can be seen. Maximum rates of net photosynthesis occur in the earlier phenological stages (in late spring to early summer), with declining rates thereafter. In this respect, *Gutierrezia* is similar to *Artemisia tridentata* measured on the same site in 1971 (results summarized in Caldwell et al., 1973). However, *Gutierrezia sarothrae* generally appears to have much higher absolute rates than *Artemisia tridentata*. This is especially interesting when viewed with the fact that the *Gutierrezia* was uniformly at much lower (more negative) water potentials than *Artemisia*. In late summer at high temperatures when net photosynthetic rates in *Artemisia* were practically nil or even negative, *Guierrezia* exhibited remarkably high assimilation rates.

Gutierrezia sarothrae did not appear to show any noticeable shift in optimum temperature for photosynthesis from one period of the season to another, as did *Artemisia tridentata* and *Atriplex confertifolia* in earlier studies. The temperature optimum seemed to stay in the 16-19 C range for the entire season, with only minor variations.

The net photosynthetic response of the grass *Agropyron spicatum* var. *inerme* under conditions of constant irradiation and variable temperature can be seen in Figure 2 for phenological stages 3 and 4. A definite peak in primary production rate can be seen in the earlier phenological stage (3 -- May), with a decline in the abolute rates thereafter. Following phenological stage 4 (late June) this species appeared to become photosynthetically inactive for the remainder of the season. This period was marked by discoloration and die-back of leaf material, extremely low (negative) water potentials and rather low, uniform daytime respiration rates (presumably from main stalks and seed heads).

As can be seen from Figure 2, peak absolute photosynthetic rates for this grass species were considerably higher than those reported for most cold desert shrub species (such as *Artemisia tridentata*, *Ceratoides lanata* and *Atriplex confertifolia* -- although not *Gutierrezia sarothrae*). This would seem to conform to the theory that, given ample moisture, grasses are more efficient producers than shrubs. A somewhat higher temperature optimum for photosynthesis (20-25 C) was observed for *Agropyron spicatum* var. *inerme* than for shrub species on the same site. There may have been a slight shift of optimum temperature to a higher level (25 C) from phenological stage 3 (May) to phenological stage 4 (June).

As shown in Figure 3, *Gutierrezia sarothrae* exhibits a similar temperature response pattern for dark respiartion to all other species studied. Absolute rates were somewhat higher in magnitude than those of other species studied on the site (*Artemisia tridentata* and *Agropyron spicatum* var. *inerme*).There appeared to be little variation in respiration rates on a seasonal basis, except at higher temperatures when respiration rates were lowest later in the season (phenological stage 7).

Figure 4 shows little variation in dark respiration rate for *Agropyron spicatum* var. *inerme* between phenological stages 3 and 4. The usual pattern of increased rate with increased temperature can be seen here. It might be mentioned that later in the season when the species became largely inactive, much lower respiration rates in a similar pattern were observed.

Effects of Temperature and Plant Water Potential on Gas Exchange and Leaf Resistances to Gas Flux of *Gutierrezia sarothrae* and *Artemisia tridentata* (preliminary)

Seasonal patterns of plant water potential for *Artemisia tridentata* and *Gutierrezia sarothrae* in the field were reported in the 1972 progress report (Caldwell et al., 1973). In 1973 some effort was devoted to determination of daily fluctuations of plant ψ for these two species. The results of pressure bomb measurements over a "typical" two-day period in August are shown in Figure 9. The pattern for both species appears to be the same, although *Gutierrezia* has lower (more negative) absolute values of ψ than *Artemisia* under the same climatological conditions.

Figures 5 and 6 show gas exchange results for irrigated vs. non-irrigated *Gutierrezia sarothrae* and *Artemisia tridentata* in the field under conditions of constant irradiation and variable temperature. Irrigated and non-irrigated individuals of both species were at the same phenological stage, to omit possible rate variations due to differences in phenology. Figures 5 and 6 show the net photosynthesis of both *Gutierrezia* and *Artemisia* to decline at higher than optimal temperatures and lower (more negative) plant

water potential. However, *Artemisia tridentata* (Fig. 6.) is much more adversely affected, and even exhibits negative net photosynthesis at higher temperatures in the low ψ (non-irrigated) treatment. A similar negative net photosynthesis was reported for this species in later summer at high temperatures in the 1972 report (Caldwell et al., 1973). A major goal of the 1973 study was to determine why this occurs.

Preliminary results are showing a greater sensitivity of r'_m and $r'_a + r'_s$ to changes in plant ψ in *Artemisia* than in *Gutierrezia*. In addition, stomatal diffusion resistance ($r'_a + r'_s$) of *Artemisia* appears to be much more responsive to higher temperatures than that of *Gutierrezia*. Figures 10 and 11 show this latter phenomenon. Photosynthesis rates and leaf resistances of *Artemisia* and *Gutierrezia* at the same plant ψ are given under conditions of constant irradiation and variable temperature. Photosynthesis rates can be seen to be much higher in *Gutierrezia*. As mesophyll resistances of the two species can be seen to be quite similar under these conditions (relatively high plant ψ), the major reason for the lower photosynthesis rates of *Artemisia* can be seen to lie in its higher stomatal diffusion resistance ($r'_s + r'_a$), particularly at higher temperatures.

The negative net photosynthesis rates observed at high temperatures and low plant ψ's in *Artemisia*, however, would have to be a function of increased r'_m values under such conditions (although the higher $r'_a + r'_s$ values mentioned previously could act to decrease photosynthesis to a certain extent). Preliminary results show the increase in r'_m at lower plant ψ and higher temperatures to be much greater in *Artemisia* than in *Gutierrezia*. A plausible explanation of this great increase in r'_m with decreasing plant ψ in *Artemisia* may lie in the fact that the decrease in net photosynthetic rate has been found to be much greater than the decrease in rate of dark respiration. Hence, at low plant ψ and high temperatures, respiration rate (dark + photorespiration) exceeds photosynthesis rate, resulting in negative net photosynthesis.

Preliminary results seem to indicate a somewhat unexpected difference in response of dark respiraton to changes in plant water potential between *Artemisia tridentata* and *Gutierrezia sarothrae*. Dark respiration rates appear to decrease with lowered plant ψ in *Artemisia* (Fig. 8), while just the opposite appears to hold true for *Gutierrezia* (Fig. 7). Data compilation is presently incomplete with respect to this problem, however. It appears as though the relationship between plant ψ and dark respiration rate may vary according to the position of the plant in the water potential continuum. That is, respiration rates in *Gutierrezia*, for example, may decrease with lowered plant ψ at relatively high (less negative) ψ and increase with lowered plant ψ at relatively lower (more negative) ψ.

Results of the defoliation gas-exchange experiments are yielding some very interesting insights into the relative contribution of stems and leaves to total shoot gas exchange. The results also indicate the possible extent of variation from one shrub species to the next regarding these relative contributions. The stems of *Artemisia tridentata*, as shown in Figure 12, appear to be relatively inactive in gas exchange, contributing little net photosynthetic activity compared to leaves, even at optimal temperatures. Stems of *Gutierrezia sarothrae* are very active photosynthetically (see Fig. 13), and thereby appear to be an important organ from the standpoint of total shoot gas exchange. There also appears to be a higher optimum temperature of photosynthesis of stems (25 C) compared to leaves (20 C). The result of this is that a significant portion (12-21 %) of total gas exchange of a typical *Gutierrezia* shoot at higher temperatures is attributable to stems.

The results of the defoliation experiments may have some definite bearing on the mode of expression of shoot gas-exchange rates for purposes of the Desert Biome. All previous reports of shoot gas-exchange rates for cool desert species have been expressed in terms of leaf dry weight or area, while actually being a representation of total shoot (leaf and stem) gas exchange. This raises the possibility that stem gas exchange should be taken into account separately. With species such as *Artemisia tridentata*, which show relatively low stem gas exchange, such an adjustment may not be necessary (Figs. 15 and 16). However, with species such as *Gutierrezia sarothrae*, possessing relatively high stem gas-exchange activity, lack of an adjustment could produce large errors in the expression of a "true" leaf gas-exchange rate (Figs. 14 and 16). Such errors in the past may have been a partial cause for seemingly invalid leaf resistance data.

Another point of concern for the Biome modelling effort is the expression of shoot gas-exchange rates. The defoliation experiments have shown stem material to be quite important with respect to total shoot gas exchange in certain cases (e.g., with *Gutierrezia sarothrae*); therefore, it would seem that some measure of stem material present should be included in the expression of gas-exchange rates. In Figures 12 and 13, two possible methods are shown for *Artemisia tridentata* and *Gutierrezia sarothrae*. The first method involves plotting leaf rates on a per-unit stem material basis, separately. This method is theoretically the best, as it would yield separate, accurate plant gas-exchange totals for both stems and leaves. However, it would involve somewhat tedious and questionable extrapolations to convert previously-collected data to such a representation, and might involve further detailed validation studies to prove stem vs. leaf gas-exchange contribution for species other than the two reported here. The second method would involve expressing total shoot gas exchange on a per-unit total shoot material (stem + leaves) basis. This method is technically quite simple, since most rates already reported are actually total shoot rates. However, it, in effect, assumes that the ratio of stem to leaf material for each of the species involved is quite constant, and this assumption may not be valid in all cases.

Photosynthesis and Water Potential Relationships of *Atriplex confertifolia* and *Ceratoides lanata*

Although there is considerable scatter in the data depicting the relationship between soil moisture potential

and photosynthesis of *Atriplex confertifolia* and *Ceratoides lanata* (Figs. 17 to 22; A3UCB10), the regression relationships derived in each case do give an indication of the linkage between soil moisture potential and CO_2 exchange. Much of the scatter is undoubtedly due to the variance associated with sampling water potential of the soil-root mass (even though four to five thermocouple psychrometers were used in each pot) and individual plant variability in stomatal behavior. This plant-to-plant variability in the desert shrubs has been a constant feature of the gas-exchange characteristics measured in earlier years of this study. It is of significance that both species are able to carry on approximately the same amount of CO_2 uptake in extremely dry soils. If anything, *Ceratoides* might be somewhat more efficient at low ψ and high temperatures.

Laboratory Carbon-14 Balance Studies

The partitioning of carbon-14 in the closed-system laboratory experiments (see Figs. 23 to 32) indicates substantial differences between the three species studied in terms of carbon allocation. The two species possessing C_3 photosynthesis (*Ceratoides lanata* and *Artemisia tridentata*) expended much more carbon in above- and below-ground respiration (44 to 61%) as compared to *Atriplex confertifolia*, possessing C_4 photosynthesis, which expended only 11 to 13%. Because of the lack of apparent photorespiration in C_4 species, the reduced daytime efflux of $C^{14}O_2$ might be expected; however, the much lower rates of below-ground respiration are less easy to explain. This is particularly perplexing since *Atriplex* invested a very high proportion of its fixed carbon in the root system as compared to the other species. The amount of carbon invested in various above-ground parts varied substantially between individual plants as well as among species. These differences in carbon allocation to various plant parts probably reflect, in large part, the exact stage of growth and should be considered in this context. More of this type of experimentation seems warranted in order to determine carbon balances for these species under a variety of growth stages.

Field Translocation and Allocation Experiments

Results of the field carbon-14 translocation studies (Tables 1 through 4) indicate an excellent consistency among the three plants chosen for detailed analysis in each harvesting period. For the above-ground portions of these plants, allocation of carbon at different times of the year seems to correspond reasonably well with the expected growth and phenological patterns for both *Ceratoides lanata* and *Atriplex confertifolia*. For example, in the April treatment, the concentration of radioactive carbon was highest in buds and new expanding leaves. Later in the season this concentration of carbon-14 dropped off considerably. The low concentration of radioactive carbon in the April treatment, when our root observation chambers indicated maximum root growth activity, would seem consistent with the hypothesis that the carbon-14 was being widely distributed to a number of growing sites and therefore the concentration was low. Later in the season, the concentration of carbon-14 in the root systems increased. Since these values only render the concentration of radioactive carbon in various plant parts, they are of limited utility when considering allocation of carbon on a community basis. Therefore, the allocation experiments were also conducted whereby concentrations of carbon-14 to above- and below-ground plant parts could be multiplied by a factor of total biomass per unit area in these different components. These allocations of carbon at the community level for these stands dominated by *Atriplex confertifolia* and *Ceratoides lanata* are given in Tables 6 and 7.

Productivity

The translocation and carbon allocation experiments carried out in the field are useful in determining the partitioning of fixed carbon at various times of the year to sites of plant growth and carbon storage. However, on an annual basis the use of carbon in root and shoot growth and plant organ maintenance cannot be determined by such values or by estimates of living biomass in different components of the plant community. Estimates of new shoot growth during the season are reasonably derived from harvests of new twig and leave growth following the completion of shoot growth during the growing season. This leaves only the radial growth of secondary woody tissues on the lower main branches and crown unaccounted for. Because of the anomalous pattern of formation of secondary xylem and phloem in *Atriplex* and *Ceratoides*, determination of radial growth increments is virtually impossible in a field situation. It is estimated, however, that radial growth of secondary tissues would account for a rather small proportion of new carbon invested in annual productivity of above-ground plant parts, especially for *Ceratoides lanata*.

Below-Ground Productivity

Because root/shoot biomass ratios in these salt desert shrub communities are on the order of 3:1 to 4:1, the importance of assessing below-ground productivity is readily apparent. Classically, below-ground productivity has been estimated by the maximum difference between minimum and maximum below-ground biomass during the course of an annual cycle. Another classical experimental technique is the determination of the amount of biomass reinvading root-free soil cores. Both techniques, however, have the principal disadvantage that sloughing or dieback of roots and subsequent regrowth are not taken into account. In water-limited ecosystems such as the salt deserts, elements of the fine root system may only function for a period of a few weeks and then become inactive and eventually decompose. If this is the case, reinvasion of the same soil mass would be necessary for extraction of water. Furthermore, in very dry soils, movement of water in the soil in response to water potential gradients is not significant. Therefore, new root extension is probably a continually necessary process for water acquisition by the plant. Observations in the soil-root chambers taken in the field indicate that the meristematic activity of individual apical regions of individual root elements is usually limited to a period of a couple of weeks. At a later time, lateral meristems may become active, but again these are limitied to approximately a two-week period of growth, even though

the entire root system may function for a period of at least six months during the year. It is, however, not possible to tell how long individual fine roots live or are functional in water and nutrient absorption. In our studies for 1973 we have attempted three basic methods of estimating aspects of productivity of the underground plant system.

The first technique was a measure of CO_2 efflux from the soil surface. Unfortunately, it is apparent that sampling of CO_2 efflux in these studies was probably initiated too late during the season. In April, there was a 10-fold decrease in CO_2 efflux followed by steady low rates of CO_2 emission for the remainder of the season during which measurements were made. During the 1974 season, CO_2 efflux will be followed during the entire calendar year in order to pick up periods of activity when it might occur in late winter and early spring as temperature and moisture conditions become favorable. Sampling adequacy appears to be a minimum problem in these soil respiration studies since the variability not only among samples, but also between under-canopy and interspace areas, is very small.

A second estimate of below-ground productivity involved a measure of reinvasion of roots into root-free soil cores. These cores were initially extracted in the beginning of the growing season, 1972, and replaced after removal of the roots from the soil. The data in Table 7 indicate the amount of root material reinvading these cores at two different depths between spring of 1972 and autumn of 1973. Although the standard errors for these samples are within reasonable limits, the validity of this technique when employed either with or without the nylon sock to contain the root-free soil column is still questionable. The soil physical environment is certainly disturbed by excavation and replacement of the soil. Also, regrowth of the root system certainly would not be the same as the normal productivity and turnover of the root system in the absence of such disturbances. If the root system is at all analogous to the shoot system, the regrowth of roots following the excavation and soil replacement would certainly not be the same as the normal growth patterns and turnover rates in undisturbed conditions. As was stated earlier, this technique also does not provide for an estimate of the sloughing or dieback of roots, and hence is not a true estimate of turnover even if regrowth within the soil cores were following a pattern similar to normal growth in undisturbed soils. Since this root reinvasion assay was conducted over a two-season period, some sloughing or dieback and decomposition of dead roots would certainly be expected to occur.

The higher apparent biomass of roots reinvading soil cores without a nylon sock as opposed to that of cores with the nylon sock to contain the soil columns is somewhat perplexing. One hypothesis might be that the presence of the nylon sock inhibited to a certain extent reinvasion of roots into the soil core. There is, however, the problem that without the nylon sock, re-excavation of the same core is not as precise as might be desired. If the core auger were cutting into undisturbed portions of the soil profile and including undisturbed segments of the root system, it would be expected that the resultant core biomass might be higher than the biomass of the columns within the nylon socks, but not as high as cores from the undisturbed community. For *Atriplex confertifolia* the cores from the undisturbed community at the 0 to 30 cm depth were conspicuously less than in the root-free cores without nylon socks.

A new technique was also applied this year to estimate the actual under-ground productivity and turnover rates. As far as can be ascertained, this is the first time that this technique has ever been used in any natural ecosystem to evaluate root turnover. As was explained earlier in this report, the basis of this technique is to determine the change in relative C^{14}/C^{12} ratios of cell wall tissues of roots between the beginning and the end of the primary growing season. The plots were labeled only once at the beginning of the season with $C^{14}O_2$. These values are shown in Table 8. A turnover coefficient was then calculated based on the change in this ratio per-unit dry weight of the roots. This turnover coefficient can then be multiplied by the initial under-ground biomass (living plus dead materials) to determine the total turnover or below-ground productivity. There are, of course, a number of assumptions and possible errors involved with this technique. The C^{14}/C^{12} ratios were determined only for cell wall tissues because it is assumed that carbon in these tissues represents purely structural carbon which will not be translocated to other parts of the plant at any other time during the season and will only be lost during the course of death and subsequent decay of these roots. All possible precautions have been taken to prevent any contamination of the cell wall material by other radioactive carbon in the original root samples. This, however, does remain as a possible error. If the contamination factor were greater at the beginning of the season as opposed to the end-of-season sample, this could result in overestimation of the turnover coefficient. Most of the other possible errors, however, result in an underestimation of the turnover coefficient. For example, it would certainly be expected that new carbon-14 would be incorporated into cell wall materials in the root system between the time of the first sampling and the end-of-season sampling, since carbon-14 was stored in other parts of the plant, and, as indicated in Tables 1 to 4, the concentration of total carbon-14 per dry weight of plant material in the roots did not increase between April and September for the plots labeled in April. This, however, would cause underestimation of the turnover coefficient and is a problem that cannot be avoided since the remainder of the plant is left intact during the season.

Another possible error leading to underestimation of the turnover coefficient is coupled with the fact that it is impossible at the present state of technology to separate live from dead root materials as was indicated in the Methods section. Therefore, this measure of C^{14}/C^{12} ratios in cell wall material had to be carried out for a root biomass sample which necessarily included dead as well as living material. At the point of the first sampling which was only a few days following labeling of the plant, it would be expected that very little carbon-14 would be included in cell wall materials of the dead roots. Since the dead root component would be expected to decompose more quickly than that which was living at the first sampling date, there would be a tendency for a dilution of the C^{14}/C^{12} ratios

between the first and end-of-season sampling dates to be less than if it were possible to perform these ratio determinations on only living root materials. Again, however, this would result in an underestimation of the turnover factor. This passage of carbon into the live- plus dead-root component and then the outflow to humus and CO_2 which would not be included in the end-of-season sample is indicated in Figure 36. As was noted in the Methods section, at the end of 1973 we have been in the process of developing a new technique which may possibly lead to separation of live from dead root materials. A preliminary estimate based on this technique indicated that in the September sample, approximately two-thirds of the *Ceratoides* root biomass and approximately 90% of the *Atriplex* biomass was alive at this time.

Synthesis: Carbon Balance Sheets

Figures 37 and 38 depict our first attempts at construction of a total carbon balance sheet for the *Atriplex confertifolia*- and *Ceratoides lanata*-dominated plant communities under study for the past few years in Curlew Valley.* This carbon balance sheet is designed to represent only the fluxes of carbon from one component to another. The state values of carbon in biomass and litter, etc., are available but not given in this particular balance sheet. All figures are in g of carbon per m^2 per year. The percentage carbon in various plant organs and shoot litter of *Atriplex confertifolia* and *Ceratoides lanata* are taken from the earlier 1970 values of N. E. West (1972). An explanation of the basis of each of these flux rates follows.

The annual net photosynthetic carbon gain is based upon measurements of net photosynthesis of branches of *Atriplex* and *Ceratoides* taken throughout the 1970 season. These were cuvette measurements similar to those reported earlier in this report. These photosynthetic values were taken when the cuvettes were programmed to track ambient environmental conditions. Measurements were taken during part or all of 24 days distributed throughout the season from April 1 to September 30 for both species. Partial-day values were extrapolated to full-day values using coefficients derived from full-day measurements at that time of year. Using representative values from throughout the season, total carbon gain per unit foliage area for the six-month period, April to September 30, was calculated for both species. Nighttime carbon loss through respiration from shoot tissues was similarly calculated. However, fewer measurements were available for these representations. In this first approximation, foliage area index values reported in the Results section have been used to depict this carbon gain on a land-area basis. As was pointed out in the Results section, these foliage index values are extremely crude and deserve more attention in the 1974 effort. An extrapolation of photosynthetic and respiratory CO_2 fluxes to a community basis will also be carried out using foliage weight calculations in 1974. This should also help to refine the representation of CO_2 gain and loss from above-ground plant parts on a land-area basis. The photosynthetic and respiration values for *Atriplex* on a unit-area basis are considered to be particularly conservative in these presentations.

The annual carbon gain by net photosynthesis is also considered to be conservative since both *Atriplex* and *Ceratoides* retained appreciable photosynthetic capacities in measurements taken in the first half of October and those species also exhibited some carbon fixation capacity in late December in the field even following periods of extreme cold (-30 C), although the rates were extremely low (ca 0.1 mg CO_2 $dm^{-2}hr^{-1}$). Nevertheless, over long periods of time, these very low rates of photosynthesis during favorable periods between September 30 and March 30 would yield an appreciable amount of extra fixed carbon to the system. Carbon losses through shoot respiration during this cold six-month period are probably also appreciable on a long-term basis.

Carbon dioxide efflux from the soil surface is also represented in Figures 37 and 38. This, of course, represents CO_2 being given off by living root respiration as well as by decay processes from the rhizosphere as indicated in these diagrams. These values of carbon efflux are decidedly conservative. As noted in Figures 33 to 35, the measurement of CO_2 efflux in the field did not begin in 1973 until mid-April. In all three communities there was approximately a 10-fold decrease in CO_2 efflux between mid-April and the first part of May. From this point until the last of the season, the CO_2 efflux remained at very low levels. It could well be that the most significant quantity of CO_2 released from the soil surface had already taken place earlier in the spring. A continuation of these measurements throughout the entire 1974 calendar year will hopefully fill in the remainder of this estimate of the annual CO_2 efflux from the soil surface. Presumably, moisture stress is the primary factor limiting this CO_2 efflux from May onward through the season until autumn.

The magnitude of CO_2 released from the soil in the long term should be equivalent to all carbon placed underground by the higher plant system, in the form of root and below-ground organs, from above-ground plant litter incorporated into the soil, and by carbon respired by below-ground plant parts, if the system is in a steady state and there is no general accretion of below-ground biomass or soil carbon. Therefore, assuming that both of these communities are at least approaching a steady state condition, the annual average CO_2 efflux from the soil surface shuld be considerably greater. As was suggested in the Results section, there appears to be no general sampling-adequacy problems since sampling variances as indicated in Figures 33 to 35 are extremely small. The potential, too, for great quantities of carbon to be released in root respiration have been indicated by our closed-system laboratory experiments reported in the Results section (see Figs. 23 through 32).

Estimates of the proportion of CO_2 efflux from the soil surface originating from live-root respiration versus the

*The carbon budgets presented here have been refined and improved since the original submission of this report (February, 1974). A revised, updated version of this section of the project will appear in the 1975 progress report.

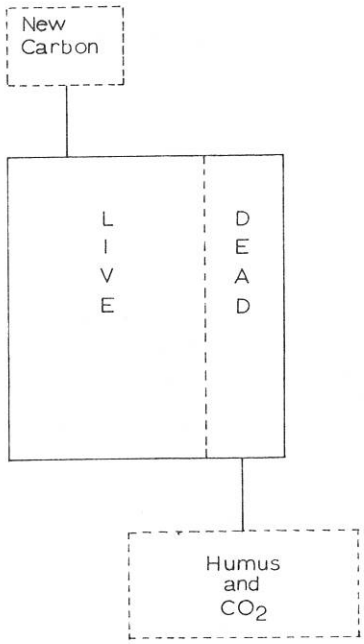


Figure 36. Depiction of carbon involved in replacement, or turnover, of the root biomass. The sampled biomass is composed in this case of living and dead, yet intact, components. The turnover coefficient is calculated by dilution of C^{14} in cell wall tissue of the biomass due to influx of new carbon. This coefficient is still applicable even though for a particular year new carbon efflux may not necessarily be balanced by loss of cell wall carbon to CO_2 and humus.

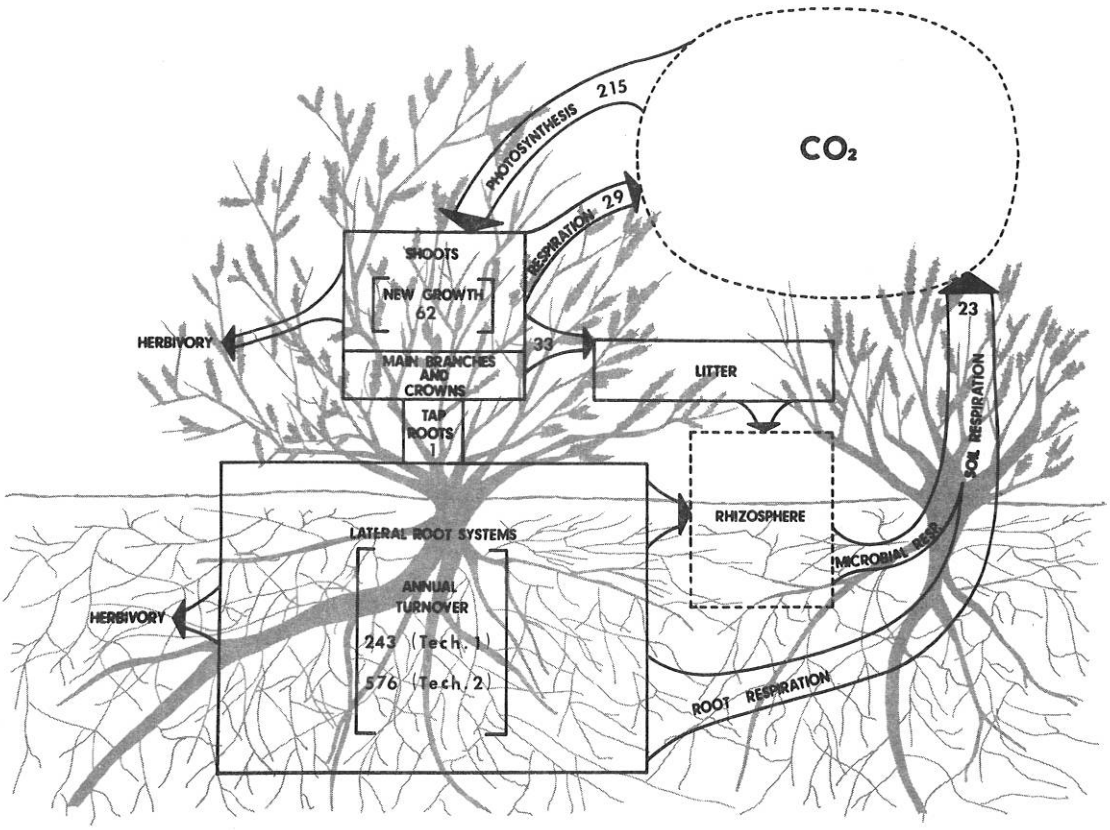
general rhizosphere respiration cannot be made at this time. It is hoped that laboratory experimentation with C^{14}/C^{12} ratios of root respiration may yield at least some clues to the proportion of CO_2 which might arise from root respiration in a field situation.

Shoot productivity data, i.e., the production of new leaves and twigs, are represented also in Figures 37 and 38. These were taken simply from the biomass harvests in July when shoot growth had terminated for both species. Although this measure is quite direct, it is undoubtedly somewhat conservative since it cannot encompass any litter which might have been dropped from the current year's growth before the time of the July harvest. This is, however, considered to be quite minimal. Carbon invested in radial growth of large woody branches or the crowns of these plants cannot be estimated in the present scope of this synthesis. The secondary growth of both of these species is constituted by an anomolous pattern of phloem and xylem. Therefore, it is impossible to determine the age or annual radial growth of the heavy woody segments of these plants. In any case, the amount of carbon invested in radial growth is considered to be quite small, particularly for *Ceratoides lanata*.

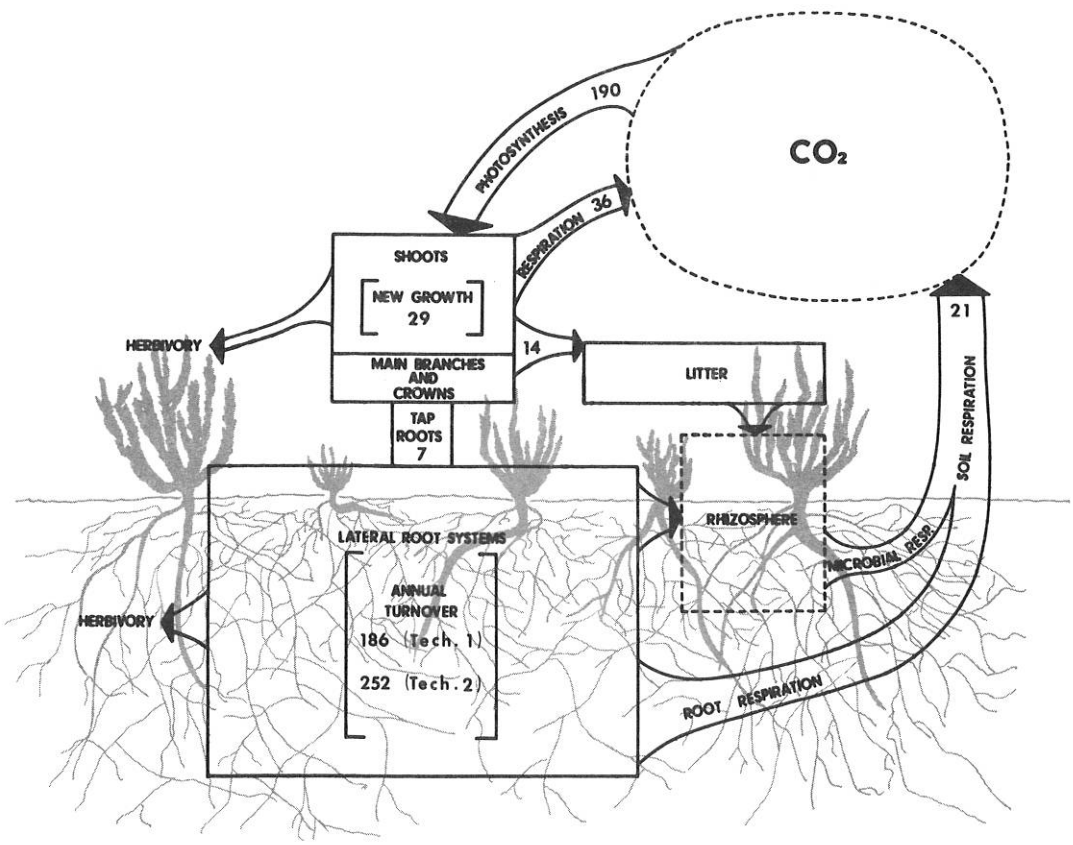
The annual carbon contained in shoot litter is also represented for both species in Figures 37 and 38. These data were taken from 1973 values by N. E. West and colleagues. These values would appear to be very conservative since it should be expected that, in a steady state situation, the annual increments of shoot litter should at least be roughly equivalent to the annual shoot productivity. Since the plants in either of these communities are not considered to be generally increasing in above-ground total community biomass, these low litter production figures are difficult to explain. The litter production values from earlier years of the West studies appear to be even more conservative than this value from the 1973 study. Although there is undoubtedly some above-ground herbivory taking place by blacktailed jackrabbits and kangaroo rats at these sites, it is very doubtful that all of this discrepancy may be accounted for by herbivory. This is particularly the case when one considers that the litter traps used in West's studies would tend to minimize herbivory by even these small animals. The possible reasons for these discrepancies will be investigated further in 1974.

Below-ground productivity, i.e., annual turnover, estimates are also given in Figures 37 and 38. Two estimates are given based on the results of the two techniques used in these studies. The smaller estimate in each case (technique 1) is based upon the biomass of roots reinvading the root-free cores (without nylon socks). These values were taken from Table 7 and represented on a g carbon m^{-2} yr^{-1} basis. The higher values (technique 2) were taken from application of the turnover coefficients (see Table 8) based on the C^{14}/C^{12} dilution studies. For *Atriplex confertifolia*, the most conservative coefficient of 1.07 was used for lateral roots in all horizons rather than to employ the larger turnover coefficients in Table 8. For the tap roots, the turnover coefficients (again from Table 8) were used to estimate annual productivity of these organs. All figures for annual turnover are based on g carbon m^{-2} yr^{-1}. The assumptions and possible errors coupled with these techniques of estimating annual underground turnover have already been discussed. It is obvious that these estimates of turnover, even in the most conservative light, are still quite large, and in the present scheme exceed annual carbon input to the system by higher plant photosynthesis. Although, as was explained earlier, photosynthetic values on a community basis may also be conservative (expecially for *Atriplex*), it is still doubtful that these turnover values can be as high as these techniques presently reveal. A sizeable portion of the 1974 effort will be directed towards refining these techniques and estimates.

Although these first attempts at total carbon balance sheets for the *Atriplex confertifolia*- and *Ceratoides lanata*-dominated plant communities are far from being in actual balance, we thought it better to represent values from current measurements than to force the system to balance by the employment of "best guesses". Despite the intensive study directed to these two communities in the past few years, this first attempt at synthesis certainly indicates our need for greater understanding of ecosystem function at the primary producer level. Our future efforts will be directed at a refinement of this understanding of the carbon balance as well as mechanisms of carbon transfer at the community level. Studies of this type in natural arid land ecosystems are almost totally absent from the current literature.



Figures 37-38. Carbon balance for an *Atriplex confertifolia*-dominated community (Fig 37, above), and for a *Ceratoides lanata*-dominated community (Fig. 38, below). Carbon fluxes are shown in gC m^{-2} yr^{-1}. No state quantities are contained. (See footnote on page 57.)



EXPECTATIONS

During 1974, research in this project will continue basically along the same lines as in 1973. An understanding of the carbon balance of these Great Basin shrub communities at the community level is fundamental to any realistic attempts at ecosystem modelling. Because of this, continued emphasis should be placed on refining our knowledge of this carbon balance and the mechanisms involved therewith. Therefore, particular attention will be placed on refining our earlier photosynthetic measurements to a community basis by an interpolative photosynthetic model and also more extensive foliage-weight determinations in order to provide a better linkage of shoot gas exchange to the community carbon balance. The root turnover terms are obviously of great quantitative importance in these communities; therefore, much effort will be directed toward refinement of the C^{14}/C^{12} dilution technique and application of this technique to estimates of the turnover in these communities. In concert with this, the attempts at determining live- and dead-root ratios from below-ground biomass samples in these communities will be further refined in 1974. It is anticipated that a sufficiently good technique to allow live-dead separation with 15% accuracy might be attained. As mentioned in the Discussion section, intensive sampling of soil respiration values in the field will continue in 1974. Also, more work towards elucidating the contribution of root respiration to total carbon efflux from the soil surface will be done in 1974, primarily based on laboratory studies. The discrepancies between litter production and annual shoot productivity will also be investigated in 1974.

Studies of the root growth dynamics of these shrubs in the field and a continuation of the plant gas-exchange studies reported herein will also be conducted in 1974.

ACKNOWLEDGEMENTS

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